COMPARATIVE AGE OF GRASSLAND AND STEPPE EAST AND WEST OF THE NORTHERN ROCKY MOUNTAINS[1]

E. B. Leopold[2] and M. F. Denton[2]

Abstract

Given the taxonomic and biogeographic differences between dominant species in grasslands of the Great Plains and the palouse grasslands and steppe of the Pacific Northwest, it seems likely that the two biomes have had separate origins. Fossil leaf and seed floras and pollen data from east and west of the Rocky Mountain cordillera and pollen data from the cordillera area suggest that three distinct floristic provinces were in existence by the beginning of mid-Miocene (Barstovian) time. Montane conifer forest poor in genera typified the Rocky Mountain foothills and nearby basins, while mixed conifer-deciduous hardwood forest and *Taxodium* swamps rich in woody genera occurred in the Columbia Basin. On the Great Plains the Kilgore flora (Barstovian of Nebraska) indicates deciduous open forest and prairie dominated by species of eastern and southern affinities. Younger Neogene floras in the Pacific Northwest suggest that steppe and local grassland were beginning to be important in the Pliocene of the Pacific Northwest, while grasslands and open forest became widespread on the Great Plains somewhat earlier (late Miocene or Clarendonian–Hemphillian time). The persistence of mixed conifer and broad-leaved forest on the Columbia Plateaus suggests that this area was open to the west through about 8 Ma. Due to the increasing height of the Cascade Range and/or regional upwarping, the rain shadow east of the Cascades became increasingly effective after the Clarendonian. Many of the terrestrial herbaceous groups and some shrub taxa of xeric environments reported here from a variety of sites are unknown in the Paleogene and may have evolved during the Neogene. According to the regional pollen record, terrestrial herbs become more diverse in the late Neogene.

Recent fossil evidence has helped substantiate that the grasslands and steppe west of the Continental Divide in the Columbia Basin area are about three million years (Ma) old, about ten million years younger than similar vegetation types east of the Divide in the Rocky Mountain foothills and in the Great Plains. Biogeographic differences between the two areas are reflected in species composition and in the dominant habits of grasses. Some climatic differences between 'east' and 'west' exist, but they do not seem sufficient to account for the vegetation contrasts.

We propose that an examination of the Late Cenozoic history (Miocene to present) of the northern Rocky Mountains may help illuminate the nature of origins of the grassland and steppe east and west of the Divide. The region to the west of the Rocky Mountains, the Columbia Plateaus[3], is endowed with some of the finest and best-documented Miocene leaf floras in North America, while the region to the east, the Rocky Mountain foothills and the Great Plains, have Mio-Pliocene deposits for which pollen, leaf, and seed data are now available. To understand the history of grassland and steppe development, because they hinge on the present east/west contrasts, the following questions need to be answered: 1) When did grassland and/or steppe first develop in the northern Rocky Mountains area? 2) What were the regional patterns of climate during the time the grasslands developed? The general climatic regimes for the area can be revealed by the types of Neogene (Miocene and Pliocene) vegetation inferred from pollen or leaf data. Species identifications from the leaf and seed floras give an index of floristic patterns that can be compared with the perceived regimes.

It is our thesis that three distinct vegetation provinces had developed in the northern Rocky Mountain region by early mid-Miocene time (ca. 16 Ma): 1) a rich deciduous hardwood and montane conifer forest west of the Continental Divide and throughout the Columbia Plateaus; 2) a montane conifer forest, poor in tree genera, and with steppe elements in the Rocky Mountain foothills; and 3) a deciduous forest with ancestral grassland elements to the east and in the Great Plains.

If vegetation types east and west of the cordillera were basically different during the Mio-

[1] We thank Daniel Axelrod, H. D. MacGinitie, Harold E. Malde, Jack A. Wolfe, and Robyn Burnham for their comments, and M. Kay Suiter for typing the manuscript.

[2] Department of Botany, University of Washington, Seattle, Washington 98195, U.S.A.

[3] "Columbia Plateaus" is the official physiographic usage by the U.S. Geological Survey (1981).

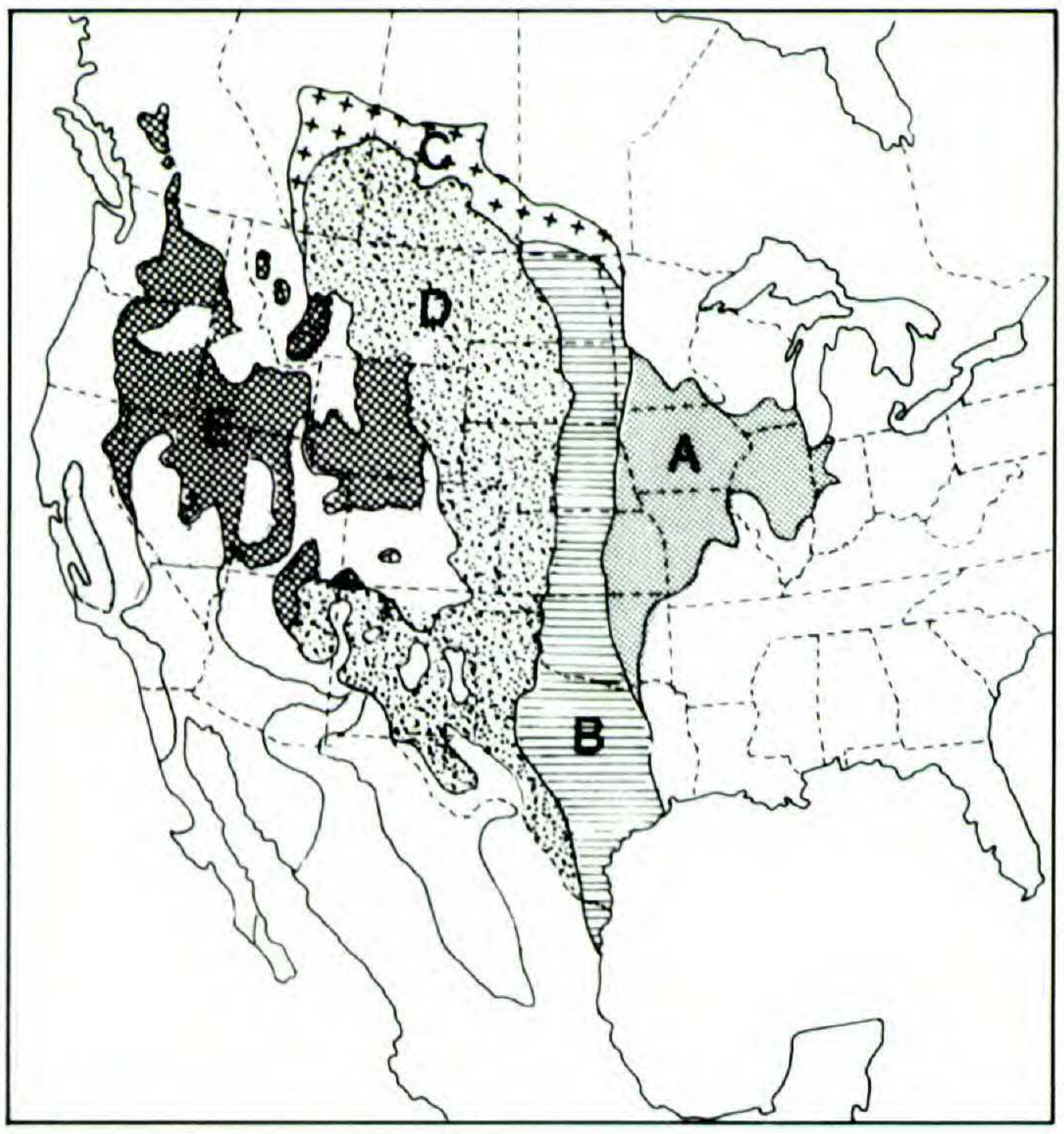


FIGURE 1. Present distribution of the chief grassland and steppe provinces in North America according to dominant taxa (from Daubenmire, 1978).—A, B. *Andropogon scoparius* province.—C. *Festuca scabrella* province.—D. *Bouteloua gracilis* province.—E. *Agropyron spicatum* province.

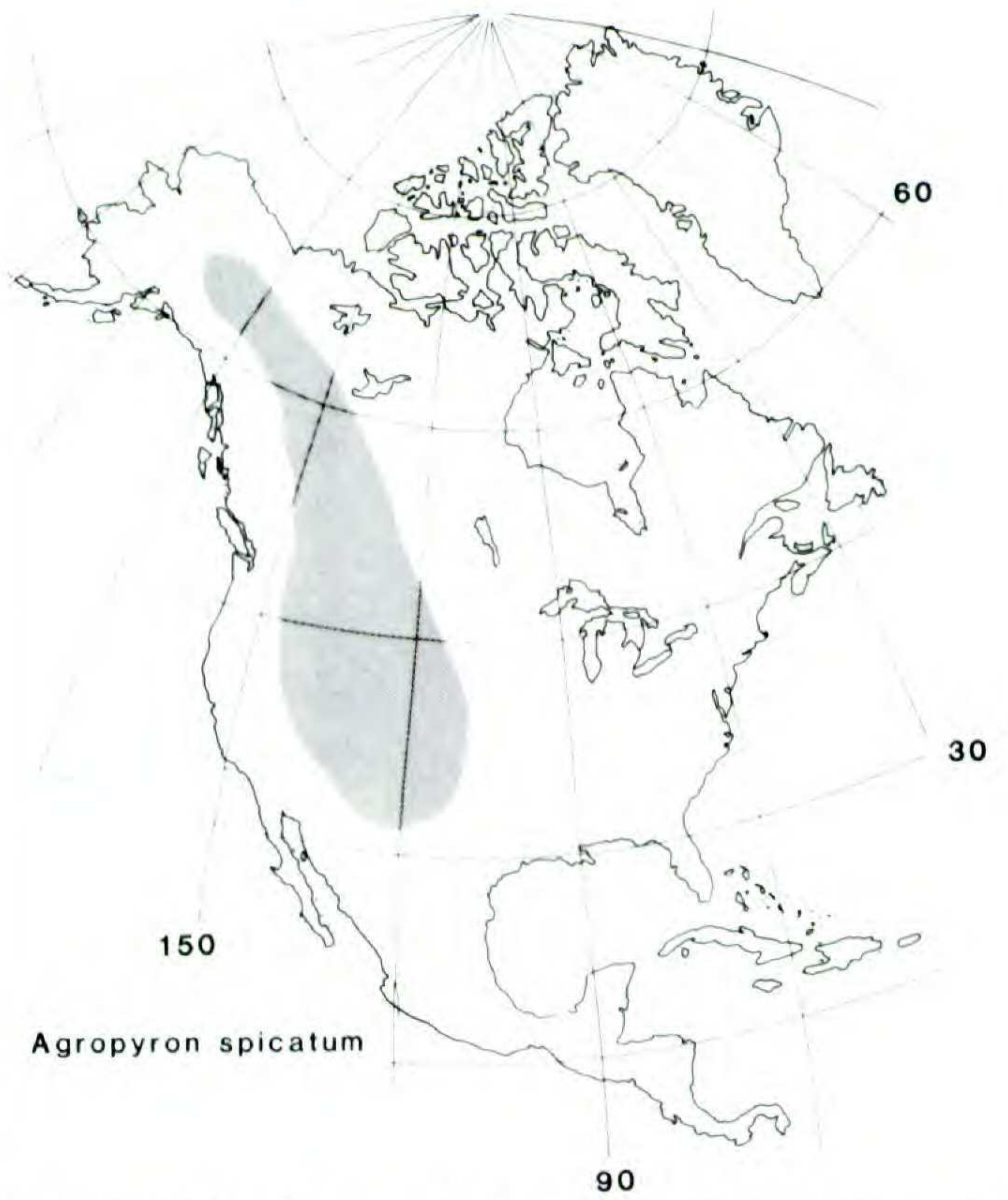


FIGURE 2. Present distribution of *Agropyron spicatum* (after Hultén, 1968; Hitchcock et al., 1969; Voss, 1972).

cene, the importance of this massif as a floristic barrier can be evaluated. Did the same species occur east and west of the divide or were they different? How do these vegetation patterns relate to the Neogene history of the region and to the development of grassland and steppe biomes?

PRESENT VEGETATIONAL PROVINCES

Figure 1 illustrates the outlines of existing grassland and steppe types in the U.S.A. On each side of the Rocky Mountain cordillera lie grasslands of different character. (1) At the eastern margin of the mid-continent grassland, there is the tall-grass prairie, a sod-forming grass association with rhizomatous root habit. The affinities of the dominant taxa, *Andropogon scoparius*, *Andropogon gerardii* (little and big bluestem), *Panicum* spp., and *Sorghastrum nutans* (Indian grass), lie to the south, in Central America, Mexico, and even South America. (2) The short-grass prairie immediately east of the cordillera, characterized by the dominance of *Bouteloua gracilis* (buffalo grass), *Aristida* spp., and others, is a province with rhizomatous and stoloniferous grasses. Most of the dominant taxa have their floristic affinities with the intermontane basins of the Rocky Mountain region. (3) To the west exists the palouse grassland and steppe of Idaho, eastern Washington, and eastern Oregon (Fig. 1), characterized by bunch grasses and steppic elements such as *Atriplex*, *Artemisia*, *Sarcobatus*, and other diverse desert-scrub genera. The biogeographic affinities of taxa in the palouse grassland and steppe are with areas to the north; for example, *Agropyron spicatum* ranges northward to Alaska and boreal regions (Fig. 2). *Festuca idahoensis* has its nearest relatives, the *F. ovina* complex, in the arctic and steppes of North America, Asia, and northern Europe (Fig. 3). *Artemisia cana* (Fig. 4) and other members of the *A. tridentata* group are mainly arctic or boreal.

Climates east and west of the Continental Divide differ significantly, chiefly with respect to the amount of summer precipitation. On the Great Plains summer rain emanates from tropical air masses moving northward from the Caribbean across this region during June and early July (Bryson & Hare, 1974). Along the southern cordillera summer rainfall occurs, especially during warm years, along the north–south path of the "Arizona Monsoon" (Neilson, 1986; Neilson & Wullstein, 1983). To the west, the palouse grassland and steppe region is characterized by a summer-dry climate, with even less summer precipitation than in the Great Plains region. The western area is dominated by the flow of dry Pacific air in summer and is in the rain shadow

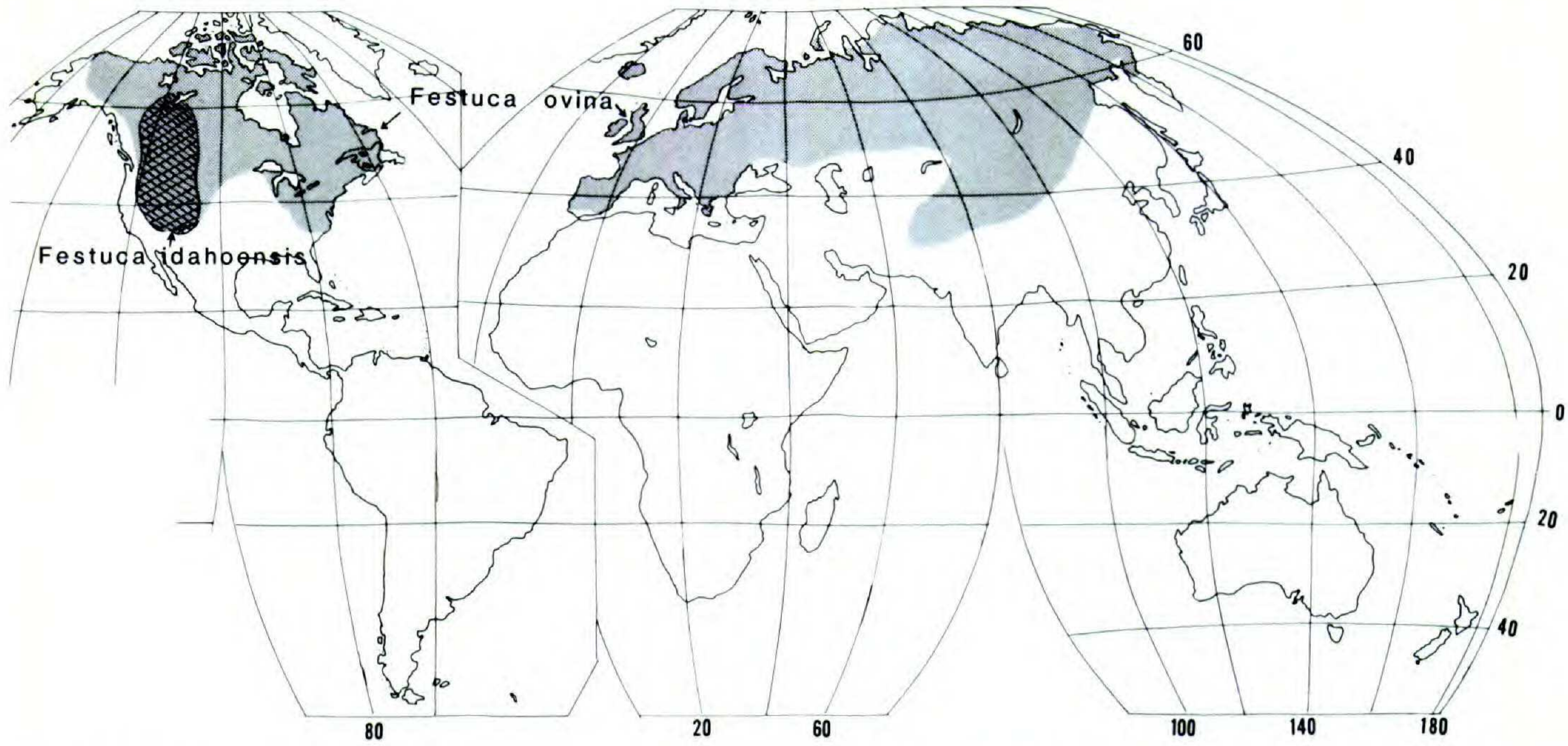


FIGURE 3. Present distribution of *Festuca idahoensis* and the closely related species *Festuca ovina* (after Hultén, 1968; Hitchcock et al., 1969).

of the Cascade Mountains; here, the distribution of grassland and steppe is limited to areas receiving less than 15–20 inches (380–500 mm) of annual precipitation, most of which falls in winter (Fig. 5).

The grassland provinces east and west of the Rockies are now dominated by separate taxa differing in geographic affinity and in growth habit (Table 1). These grasslands differ in distribution of C_4 (warm growing season) and C_3 (cool growing season) grasses. C_4 grasses are always of low frequency (less than 18%) west of the Rockies but may dominate in certain areas east of the Rockies (Mack & Thompson, 1982; Teeri & Stowe, 1976). In addition, there are fundamental differences between these two grassland provinces with respect to their carrying capacities for large, grazing ungulates; for example, the carrying capacity of the palouse grassland dominated by bunch grasses sensitive to trampling is much lower than that of grasslands east of the cordillera (Mack & Thompson, 1982). The biogeographic, physical, and climatic contrasts of these regions imply that their historical development must have been very different. This is the subject of the discussion that follows.

DATA BASE

Because our study concerns events after the early Miocene, we discuss data from sites younger than 18 Ma (Hemingfordian and younger stages). The sites are mapped in Figures 6 and 7 and are arranged according to geologic ages in Table 2.

West of the Rocky Mountain cordillera, the area of the Columbia Plateaus contains a wealth of well-documented fossil plant sites. We have studied data from 15 of these, of which four have yielded pollen data (Fig. 6). Dating is established by K/Ar isotope ratios for a few of these and by land-mammal evidence for others.

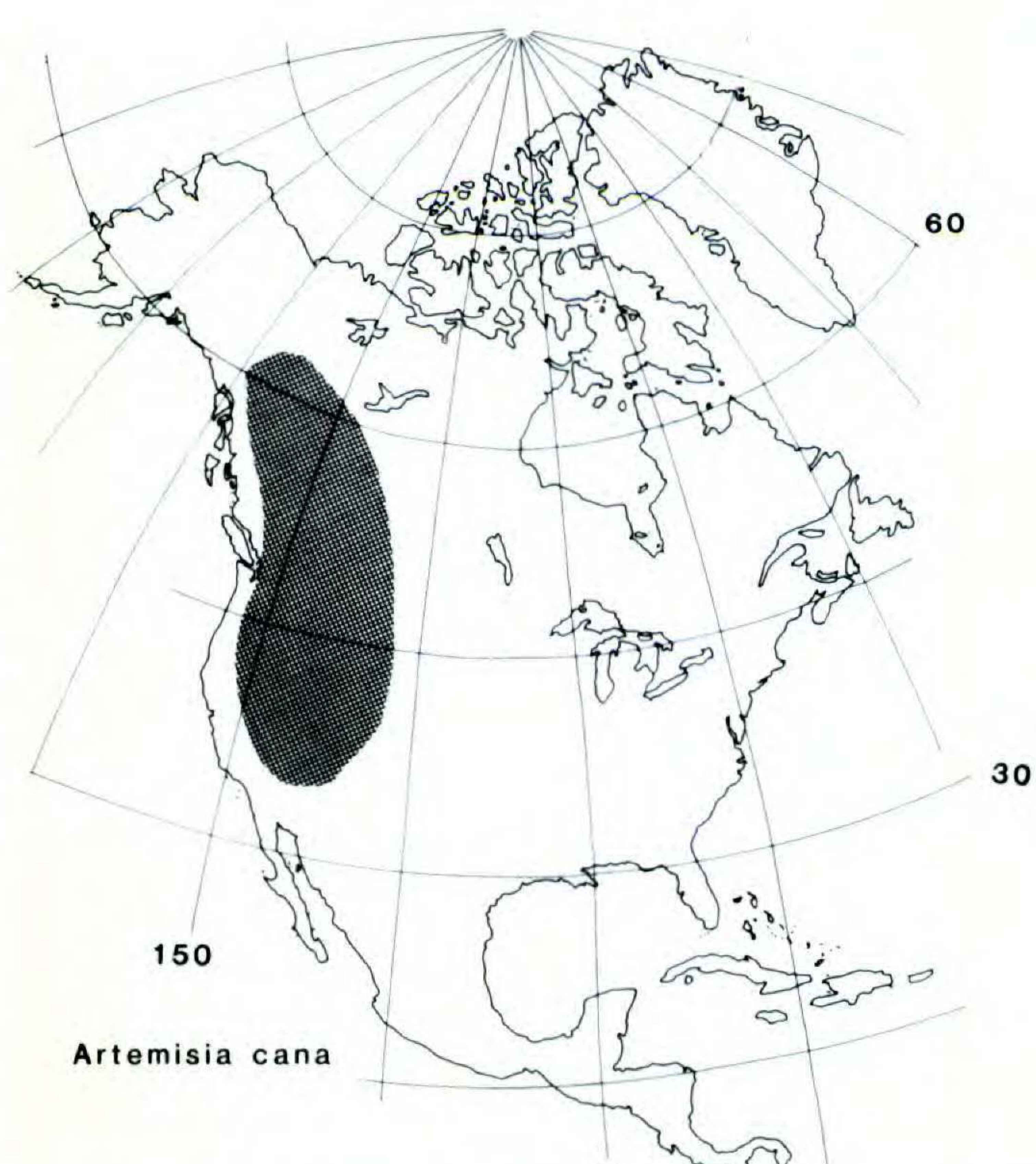


FIGURE 4. Present distribution of *Artemisia cana* (after Hultén, 1968; Hitchcock et al., 1955).

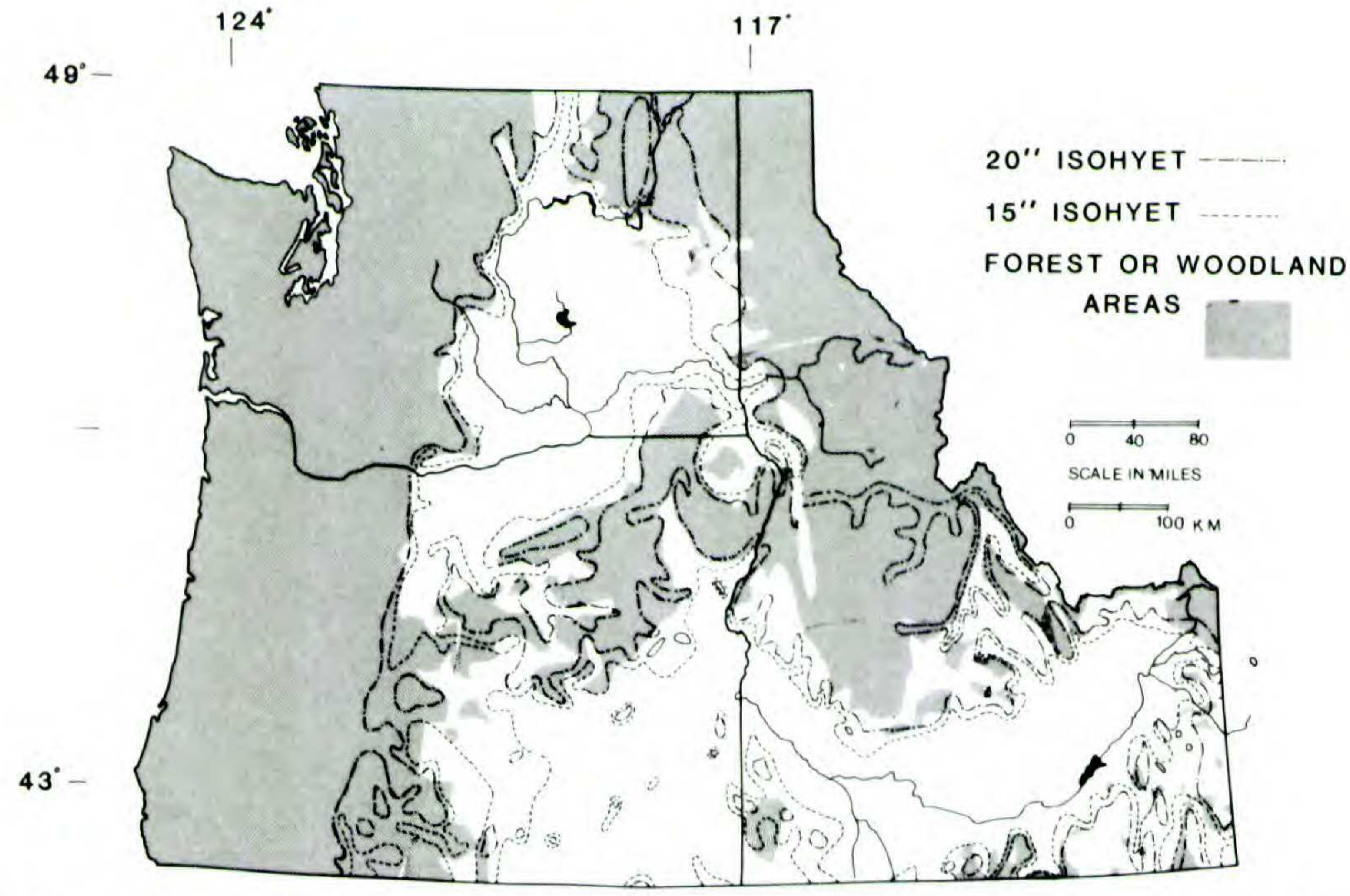


FIGURE 5. Relationship of the forest/steppe border to the 15- and 20-inch (380 and 500 mm) isohyets of annual rainfall in the Pacific Northwest (after Sherman, 1947, and U.S. Weather Bureau data).

In the foothills of the northern and central Rocky Mountains, we have four localities (Fig. 6) from which the main documentation is from fossil pollen, although some megafossil data exist (identification of taxa is on the generic level only). These floras are geographically scattered, but their relative ages were ascertained by land-mammal data.

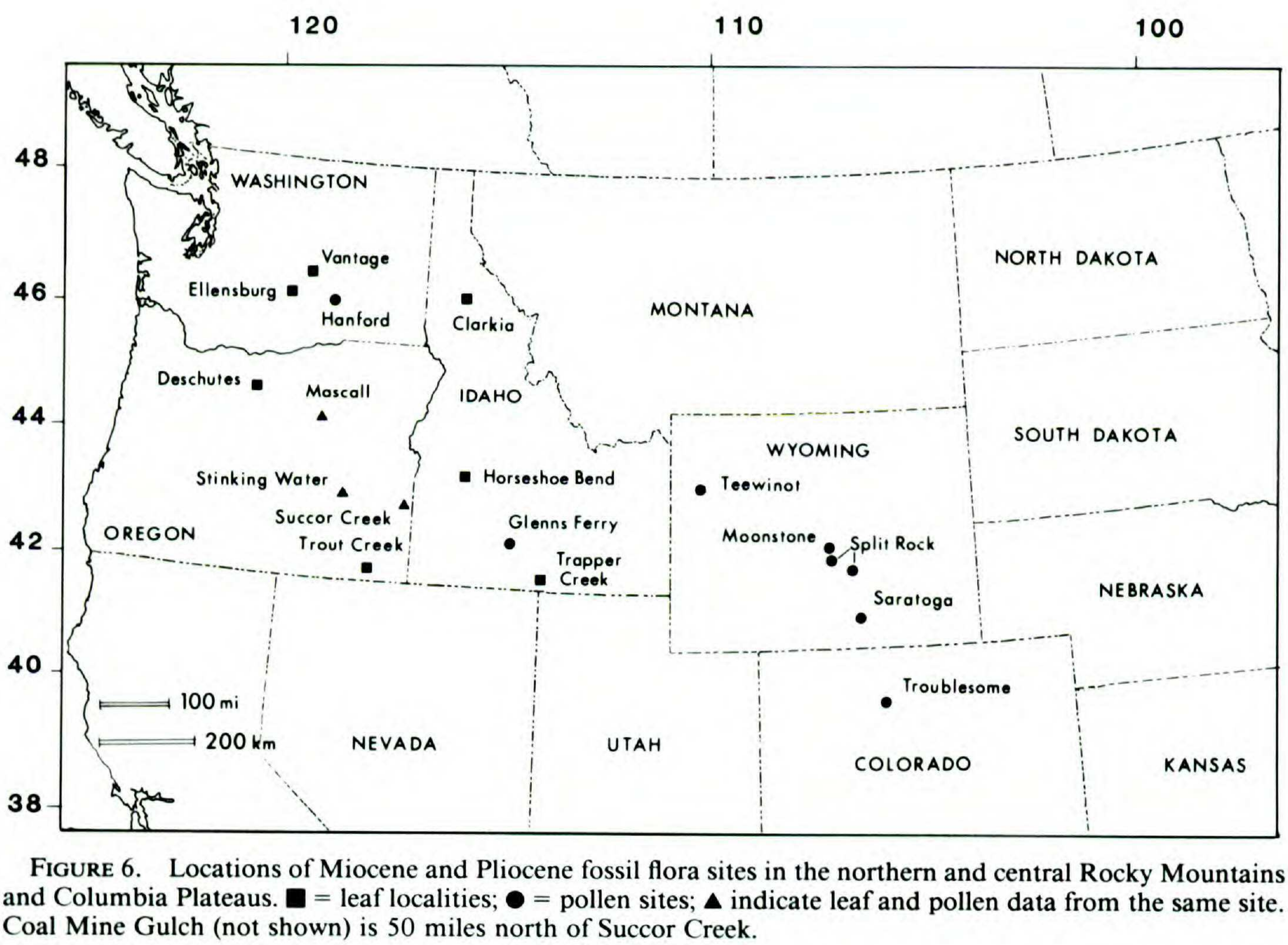


FIGURE 6. Locations of Miocene and Pliocene fossil flora sites in the northern and central Rocky Mountains and Columbia Plateaus. ■ = leaf localities; ● = pollen sites; ▲ indicate leaf and pollen data from the same site. Coal Mine Gulch (not shown) is 50 miles north of Succor Creek.

In the region east of the cordillera, there are several megafossil localities (Fig. 7) containing small leaf floras and there are abundant fruit and seed localities (Elias, 1942); recent work with pollen analysis and electron microscopy of fruiting parts, grass anthoecia, epidermal patterns, and phytoliths revealed the composition of many of these assemblages.

Miocene Vegetation Provinces of the Northern Rocky Mountain Region

Three vegetation provinces had developed by the mid Miocene in the northwestern and north-central mid-continent.

I. West of the Rocky Mountains—the Columbia Basin

A. Miocene Floras

Fifteen leaf floras of mid and late Miocene age demonstrate that mesic forest vegetation under a warm-temperate summer-wet climate existed in the Columbia Basin by about 18 Ma until Hemphillian time (about 8–4.5 Ma). Difference in warm- and cold-season average monthly temperature has been estimated at about 20°C (Wolfe, 1978). Even though important changes in climate and vegetation occurred through the main sweep of Miocene time, the major elements of the flora were not eliminated. Some chief features of the vegetation derived from the leaf flora are:

(1) Dominant vegetation (Trapper Creek[4] of Clarendonian age is an example; summary in Table 3) was deciduous hardwood forest and mixed montane conifer-deciduous forest, with some broad-leaved evergreen elements and diverse (8–26 genera) woody dicots. Shrubs were important (up to 30%), while herbaceous groups were few (only four taxa and these were generally rare aquatics).

(2) Species showed close relationships with modern elements of summer-wet areas in eastern Asia, eastern U.S.A., and/or western U.S.A. in about equal percentages. For example, at Trapper Creek modern affinities seem split between

[4] Axelrod (1964) considered the age of the Trapper Creek flora as 15–16 Ma. More recent evidence from K/Ar dating (Armstrong et al., 1975; Fields, 1983) suggests an age of 10.5–12 Ma.

TABLE 1. Chief characteristics of modern grassland types in the U.S.A.

	WEST	ROCKY MOUNTAINS	EAST
KEY SPECIES:	Grassy steppe	Short-grass prairie	Tall-grass prairie
	Agropyron spicatum	*Bouteloua gracilis*	*Andropogon scoparius*
	Poa	*Aristida*	*A. gerardii*
	Festuca idahoensis	*Buchloë*	*Panicum virgatum*
		Muhlenbergia	*Sorghastrum nutans*
		Sporobolus	
	(north temperate & boreal affinities)	(intermontane basin affinities)	(southern affinities)
DOMINATED MAINLY BY:	caespitose (bunch) grasses	rhizomatous/stoloniferous grasses	
CLIMATE:	summer dry	summer moist	

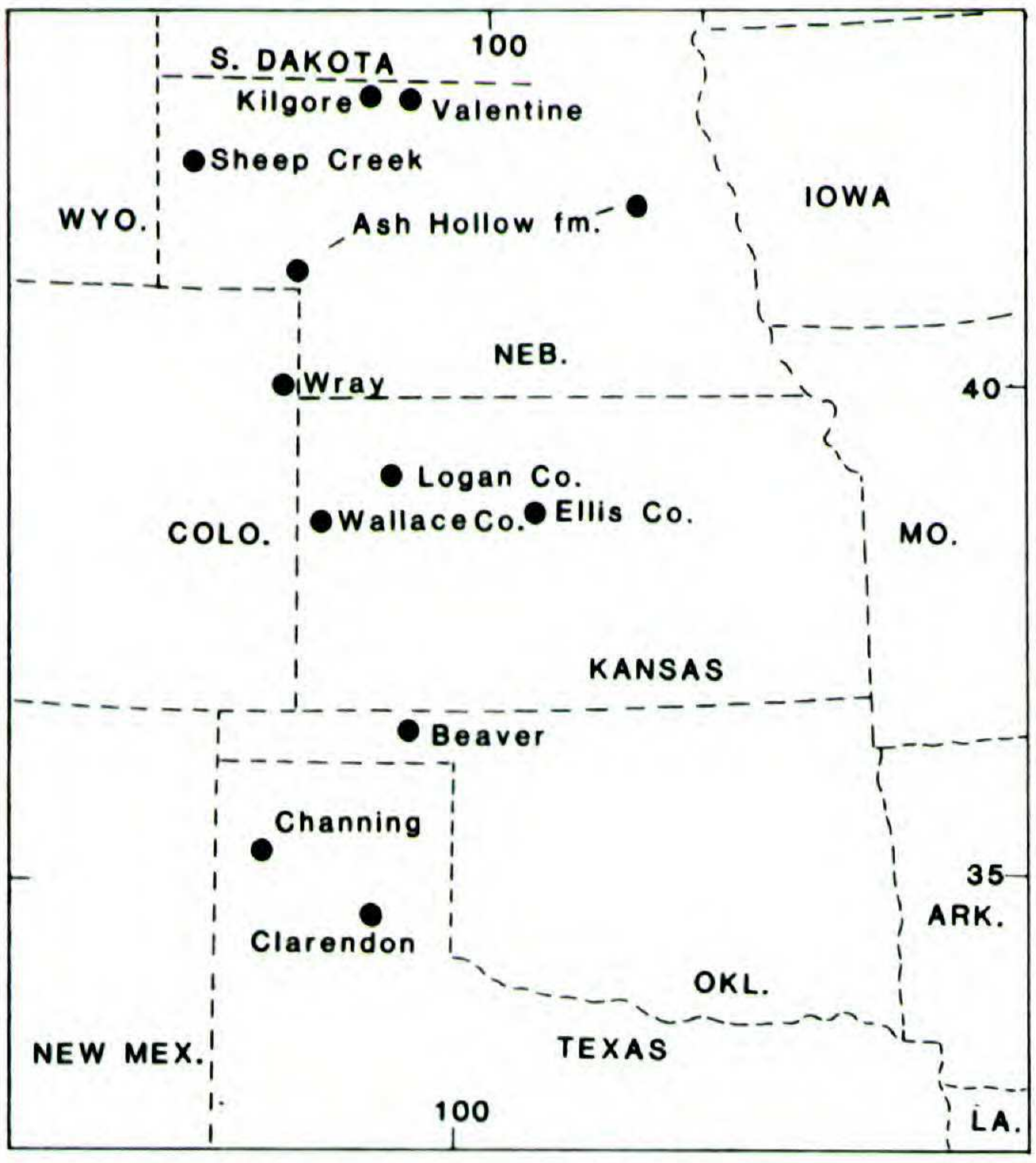


FIGURE 7. Location of Miocene and Pliocene fossil flora sites on the Great Plains (High Plains of Axelrod, 1979).

these three areas (Axelrod, 1964). There were only minor temporal changes in the role of these geographic elements through mid-Miocene time (Table 4).

(3) Vegetation was chiefly woody. Characteristic plant communities summarized for the mid-Miocene floras of southern Idaho included:

(a) Swamp forest, particularly *Taxodium* swamp with associated *Nyssa, Liquidambar, Persea, Salix,* and *Alnus.*

(b) Lake-border woodland, with *Quercus simulata* and species of *Acer, Betula,* and *Populus.*

(c) Valley forest, including some of the taxa mentioned above and a wide range of woody deciduous groups such as *Alnus, Amelanchier, Prunus, Parthenocissus, Cornus, Fraxinus, Ulmus, Pterocarya, Carya,* and *Sophora* as well as an important component of broad-leaved evergreens, such as *Quercus* (cf. *Q. chrysolepis*), *Sassafras, Berberis, Ilex,* and diverse conifers such as *Keteleeria, Picea* (cf. *P. breweriana*), *Pseudotsuga, Tsuga, Abies,* and *Sequoiadendron.*

(d) Mountain-slope forest, including many of the conifers and hardwoods mentioned in the valley forest, also *Garrya* (*G.* cf. *fremontii*), *Rhus, Ungnadia, Abies* (*A.* cf. *delavayi* or *A. recurvata*), *Abies concoloroides, Calocedrus* (*C.* cf. *decurrens*), and most importantly, *Pinus* (*P.* cf. *ponderosa, P.* cf. *monticola*), and *Cedrus.*

Some of the most frost-sensitive forms (*Liquidambar, Cedrela*) seem to disappear during the mid Miocene, especially in regions close to the Rocky Mountains. However, the occurrence of warm-temperate *Taxodium* swamp vegetation persisted in eastern Washington until ca. 8 Ma and in Idaho until ca. 12 Ma.

Although Miocene communities typically included species of eastern Asian and eastern American affinities, western American elements seem to dominate in the montane slope forest communities.

Chaney (see Chaney & Axelrod, 1959: 53) discussed the possibility that open savanna or prairie vegetation existed at some mid-Miocene sites where pollen and leaf data are available, e.g., Mascall and Stinking Water floras of eastern Oregon. Part of his rationale was based on the diverse fossil mammals whose modern relatives live in savanna habitats today (rhinoceros, horses, rodents, lagomorphs, camels, and most abun-

TABLE 2. Stratigraphic ages of Late Cenozoic floral localities of the Columbia Plateaus, northern Rocky Mountains, and Great Plains.

		Ma		EASTERN OREGON	EASTERN WASH.	SOUTHERN IDAHO	NORTHERN IDAHO	WYOMING COLORADO	NORTHERN NEBRASKA
Quaternary						Bruneau			
Pliocene		1.7	Blancan			Glenns Ferry			
Miocene	Late	4–5	Hemphillian	Deschutes		Chalk Hills			
Miocene	Late	8	Clarendonian		Hanford	Banbury Basalt		Moonstone Teewinot	Ash Hollow
Miocene	Mid	12	Barstovian	Stinking Water Trout Creek Succor Creek Mascall	Ellensburg Vantage	Trapper Creek Poison Creek Payette	Clarkia	Saratoga	Kilgore Sheep Creek
Miocene	Early	16.5 18	Hemingfordian					Split Rock Troublesome	

TABLE 3. Dominant vegetation types in Late Cenozoic floras of the Columbia Plateaus (from Axelrod, 1964; Chaney & Axelrod, 1959; Graham, 1963; Leopold & Wright, 1985; MacGinitie, 1933; Smiley & Rember, 1985; Taggart et al., 1982).

	Barstovian							Clarendonian			Hemphillian			Blancan	Quaternary
	Trout Creek	Succor Creek	Clarkia	Horseshoe Bend	Vantage	Coal Mine Gulch	Mascall	Stinking Water	Lower Ellensburg	Trapper Creek	Chalk Hills	Hanford	Poison Creek	Glenns Ferry	Bruneau & Younger
Mixed deciduous evergreen hardwood forest							X		X				X		
Deciduous hardwood forest		X	X	X					X		X				
Ecotone		X			X		X								
Montane conifer–deciduous hardwood forest	X							X		X		X	X		
Ecotone										X					
Montane conifer forest										X					
Grassland and conifer forest														X	
Steppe and conifer forest														X	X
Steppe															X
Taxodium swamp forest		X	X	X		X			X			X			

dant, the oreodonts). Direct evidence, however, is limited. Herbaceous plants are an important element in modern savanna. Aside from aquatics and ferns, herbaceous groups are rare in the Miocene leaf record of the Columbia Plateaus. Even pollen evidence indicates that herbaceous groups were limited in diversity and abundance (Appendix I); in the Mascall only two nonaquatic herb types were identified by Jane Gray (in Chaney & Axelrod, 1959: 43): "Pollen of Gramineae are present but not numerous." The situation was similar in the Stinking Water and Blue Mountains floras. Some fossil seeds and fruits were found, but these, as in the leaf flora, were all from woody taxa.

The floristic role of herbs in mid Miocene of the region is illustrated in the pollen lists from the Succor Creek Formation (14–12 Ma at the type section; Fields, 1983) in southeastern Oregon (Taggart & Cross, 1980). Six probably terrestrial herbaceous groups are recorded: *Pachysandra, Ambrosia,* Onagraceae, Amaranthaceae, Gramineae, and Umbelliferae (Appendix I). Because the pollen diagrams summarize their abundance according to broad ecological groupings, the relative importance of herbs is not documented. In their discussion Taggart & Cross made it clear, however, that grass and Compositae pollen are sporadically abundant as part of a successional cycle (see below).

TABLE 4. Percentages of element representation in mid-Miocene floras and age groups, Columbia Plateaus region (from Chaney & Axelrod, 1959, table 32; Axelrod, 1964, table 5).

	Barstovian			Clarendonian		
Geographic Elements	Mascall	Succor Creek	Trout Creek	Stinking Water	Trapper Creek	Lower Ellensburg
Eastern American	65	61	50	58	58	70
Eastern Asian	50	50	50	53	69	45
Western American	37	37	56	60	62	58
Total taxa	64	46	46	38	61	32

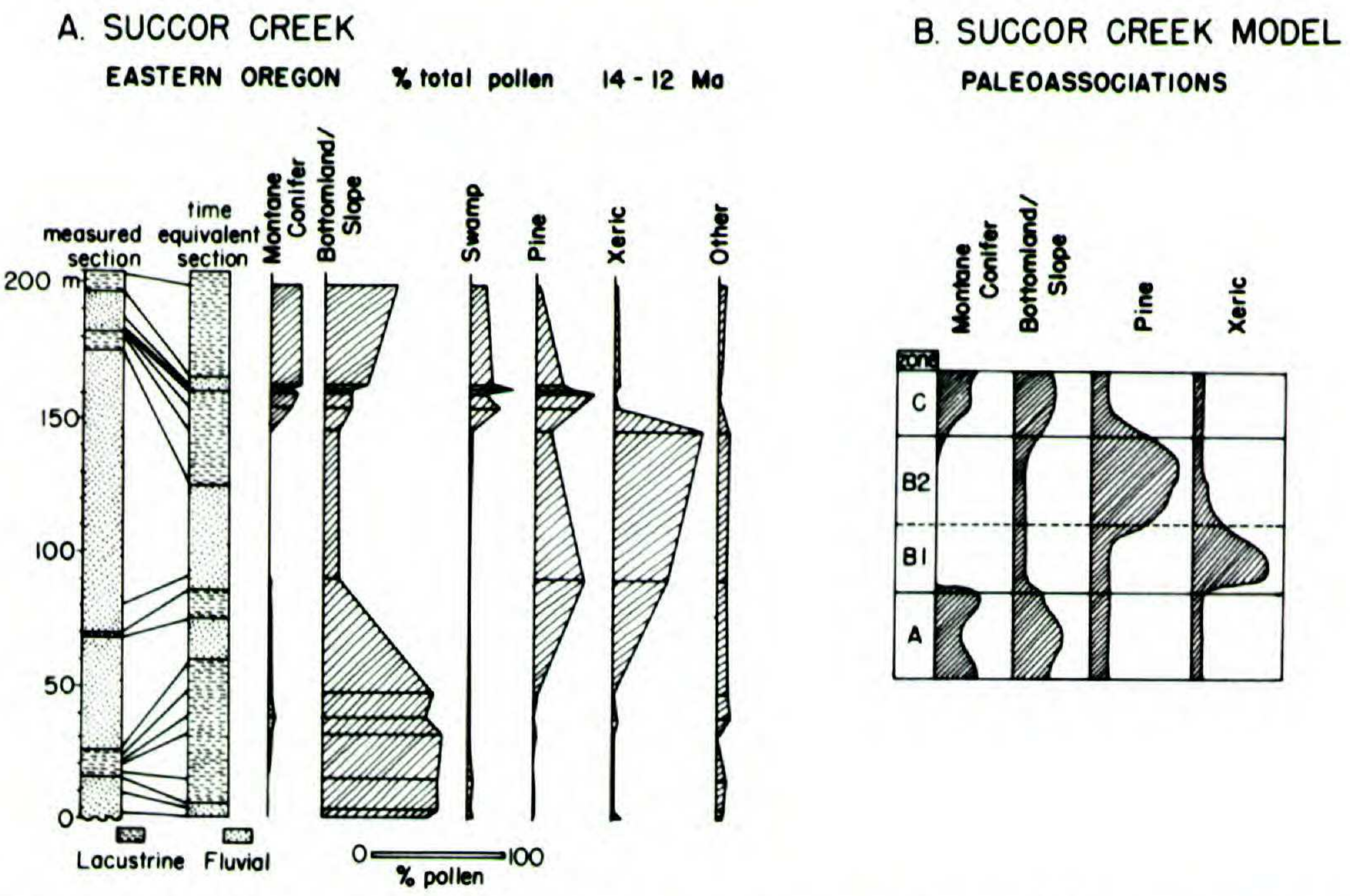


FIGURE 8. Generalized pollen diagram indicating vegetation phases in a 200–meter section at the Succor Creek flora type locality of mid Miocene age, eastern Oregon (A); a model of the successional sequence (B) is shown on right (from Cross & Taggart, 1982).

(4) Vertical arrangements of plant communities were suggested by pollen data. Many leaf floras do not demonstrate clearly that an altitudinal zonation occurred in the Miocene floras, yet pollen-stratigraphic evidence makes it certain indeed. At Succor Creek, Oregon, Taggart & Cross (1980) and Taggart et al. (1982) showed a repeated successional cycle of montane conifer forest, bottomland/slope associations, and xeric shrub with steppic elements followed by *Pinus* spp.; the sequence then reverts to swamp, bottomland/slope, and then to montane conifers. A single cycle in a 200-meter section is shown in Figure 8. The dramatic oscillations can readily be interpreted as elements from various altitudinal communities participating in an altitudinal succession caused by climatic changes. Taggart et al. (1982) believed the successional changes are related to disturbance episodes of volcanism, but it is also possible that these are forced by small oscillations of climate, or both.

At a much younger (ca. 8.5 Ma) site at Hanford in eastern Washington, floodplain sediments (lowest Ringold formation) of the ancestral Columbia River record a somewhat similar succession (Fig. 9a, b; Leopold & Nickmann, unpubl.). The sediments overlie the Upper Columbia River Basalts (10.5 Ma) and an unconformity dated at 8.5 Ma (Tallman et al., 1981; DOE, 1986: 3–40). The lithology indicates that local depositional environments were changing. In a series of cycles, fine-grained swamp deposits grade upward to increasingly coarse riparian sediments. Two pollen diagrams (core holes DC-3 and DC-7/8), each beginning in fine-grained sediments, register a rich Taxodiaceae-type (cf. *Taxodium*) swamp association. (We infer this identification because *Taxodium* is abundant in the underlying Ellensburg Formation.) This phase is followed by increases in bottomland/slope hardwoods, and finally *Cedrus* and *Pinus* dominate. Herbs and xeric elements are always present in trace amounts. Presumably in a floodplain area such as Hanford, the vegetation changes record either shifting riparian environments (edaphic factors) or changes wrought by climate. While the elevational relief of each of these forest types occupied is not clear at either site, it is possible that as much as 500–1,000 feet of relief existed at Succor Creek.

The Cascade Range was probably rising during Miocene time (McKee, 1972; Smiley, 1963), and its rain shadow eastward eventually changed the character of the vegetation from mesic and summer-wet to xeric and summer-dry. The lower Ellensburg and the Hanford floras suggest that eastern Washington was open to the west through ca. 8 Ma. This meant that the Cascades were not significant enough to block moisture from the westerlies until some time after the Clarendonian. In part this helps explain the general similarity of Pacific Northwest floras during the early and mid Miocene.

B. IMPLICATIONS FROM PLIO-PLEISTOCENE FLORAS

Given the data above concerning the characteristics of the Miocene forests of the Columbia Plateaus, when did forest vegetation diminish, allowing the development of grassland and steppe?

West of the Rocky Mountains, pollen data from Idaho demonstrate the decline and impoverishment of the Miocene forests and the development of local grassland and steppe. These changes that occurred from late Pliocene to Quaternary were surprisingly late. In lake and stream deposits of southwestern Idaho a unique and well-dated composite pollen sequence embraces parts of the last 11 million years, after Trapper Creek time through the early Quaternary (Fig. 10; Leopold & Wright, 1985). Fossil pollen in these deposits tends to be scarce, and pollen-bearing beds are hard to find (90% of our collections were barren). Some megafossils have been identified at certain sites.

In the sequence (Idaho Group) the lower sediment units are from the Poison Creek, Jenny Creek, and Chalk Hills formations and Banbury Basalt of mid and late Miocene age (Armstrong et al., 1975; Fields, 1983; Leopold & Wright, 1985; Appendix II). The floras record mixed deciduous and conifer forest with declining hardwoods; these were mainly *Ulmus* but also included *Pterocarya, Carya,* and *Juglans.* A holly-leaved oak (leaf evidence from the Poison Creek Formation) is reminiscent of that recorded at Trapper Creek (ca. 11 Ma). Wood from the Chalk Hills Formation records diverse hardwoods. Younger sediments of the Glenns Ferry Formation (ca. 3–2 Ma) containing the Hagerman lake beds record an impoverished pine and mixed conifer assemblage with rare pollen of exotic hardwoods. Steppe elements (*Sarcobatus* and other Chenopodiaceae, *Artemisia* and other Compositae) are consistently present and increase sporadically upward in this section. Peaks (up to 60%) of grass pollen are associated with the Hagerman fauna from which remains of about 100 horses (*Pleisippus*) have been found. In the upper Glenns Ferry, Chenopodiaceae and *Artemisia*/Compositae increase while tree pollen declines. Taxa of terrestrial herbs are more diverse than in the Miocene (Appendix I).

Miscellaneous Pleistocene samples from the area suggest that *Artemisia* and Chenopodiaceae are important, if not the dominant, pollen forms. Above an unconformity (see top of Fig. 10) Irvingtonian mammals including *Equus* plus K/Ar evidence date the Bruneau Formation as middle Pleistocene; a Bruneau pollen sample (D1694) shows *Artemisia* to be 50% of the count, suggesting a true *Artemisia* steppe had developed. Two other samples rich in *Artemisia* pollen (D1120 and D1698; Fig. 10), previously reported as Bruneau (Leopold & Wright, 1985), are now classified as Yahoo Clay of late Pleistocene age (Malde, 1982). The top fossil sample (D1697), showing 80% *Artemisia* and other Compositae pollen, is from a late Pleistocene soil above the King Hill Basalt.

In northern Oregon the Deschutes flora (ca. 4–5 Ma) suggests low-diversity riparian vegetation typical of unforested regions and is consistent with a decrease in summer precipitation in late Miocene time (Appendix III; Chaney, 1938).

Taken as a whole, the data indicate that steppe in the Columbia Basin probably did not develop as a major vegetation unit until after the Hemphillian (4.5 Ma). The Snake River Plain section places the change from rich (deciduous and) coniferous forests to montane conifer forest between 10 and 3 Ma. In this region steppe and palouse grassland probably became widespread for the first time in the Quaternary.

II. THE ROCKY MOUNTAIN FOOTHILLS

The lack of megafossil evidence for northern Rocky Mountain Neogene sites is unfortunate (the well-documented Clarkia flora of middle Miocene age lies in the Columbia Basin floristic province). Pollen records from the Rocky Mountains and eastern foothills demonstrate the comparatively modern aspect of plant communities there during the Miocene.

At Jackson Hole, Wyoming, the Teewinot lake deposits (predating the Teton Range) provide a long record of montane conifer forest with occasional bursts of lowland steppe and riparian types (Fig. 11; Barnosky, 1984). Presumed plant communities include:

(1) *Saline basins.* High percentages of *Sarcobatus* pollen accompany other Chenopodiineae, *Ephedra,* and sedges.

(2) *Presumed riparian* areas. These are characterized by pollen of probable phreatophytes,

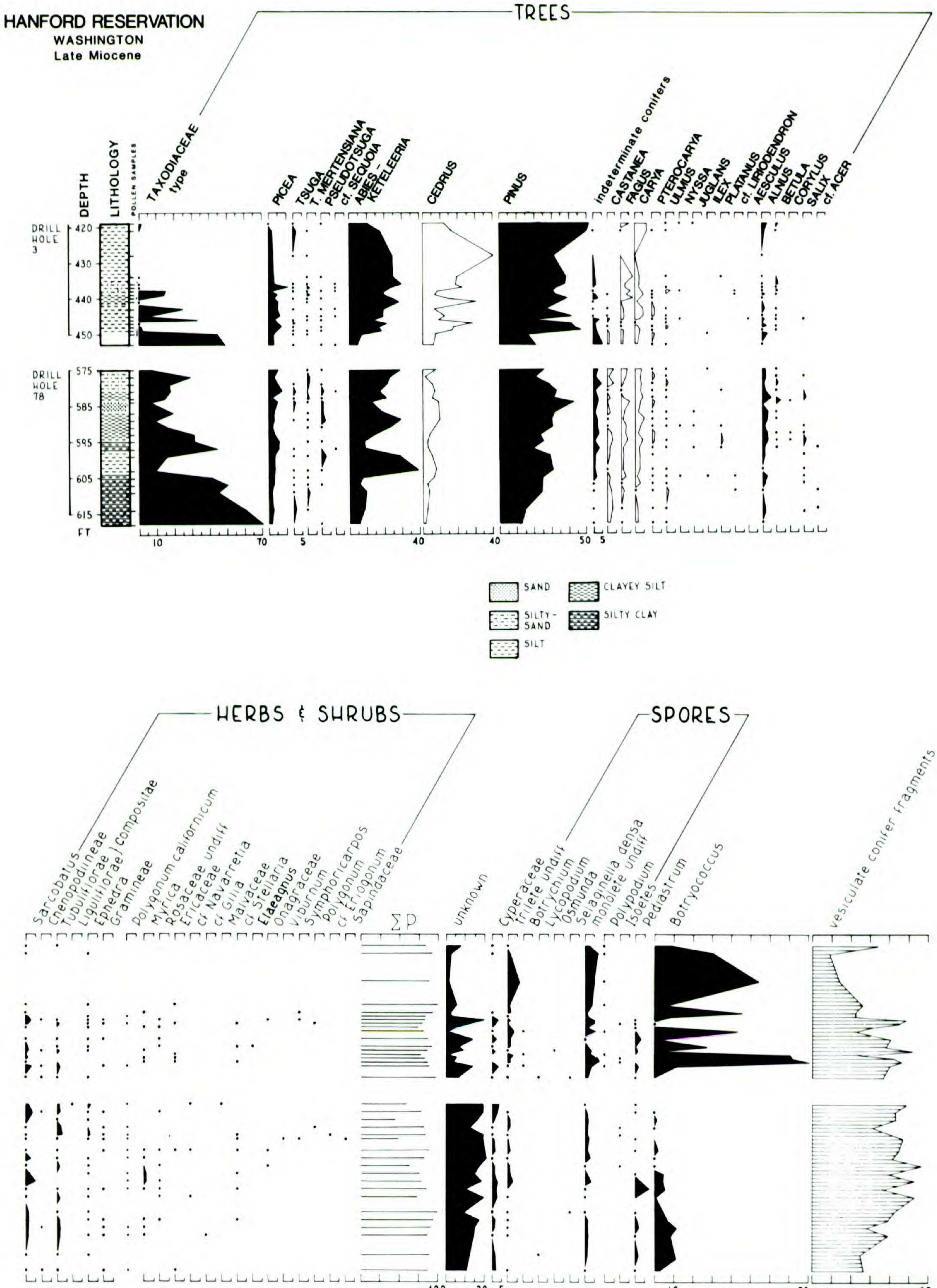


FIGURE 9A. Late Miocene pollen sequence, Hanford, Benton County, Washington. Two pollen diagrams from lowermost Ringold Formation, % total pollen (Leopold & Nickman, unpubl. data). Stratigraphic data are from Department of Energy (1986: 3–16) drill holes DC-3 and DC-78, which are correlative in age and about 12 miles apart. Depths below surface are given in feet. The sediments are dated at 5–10 Ma (probably 8.5 Ma).

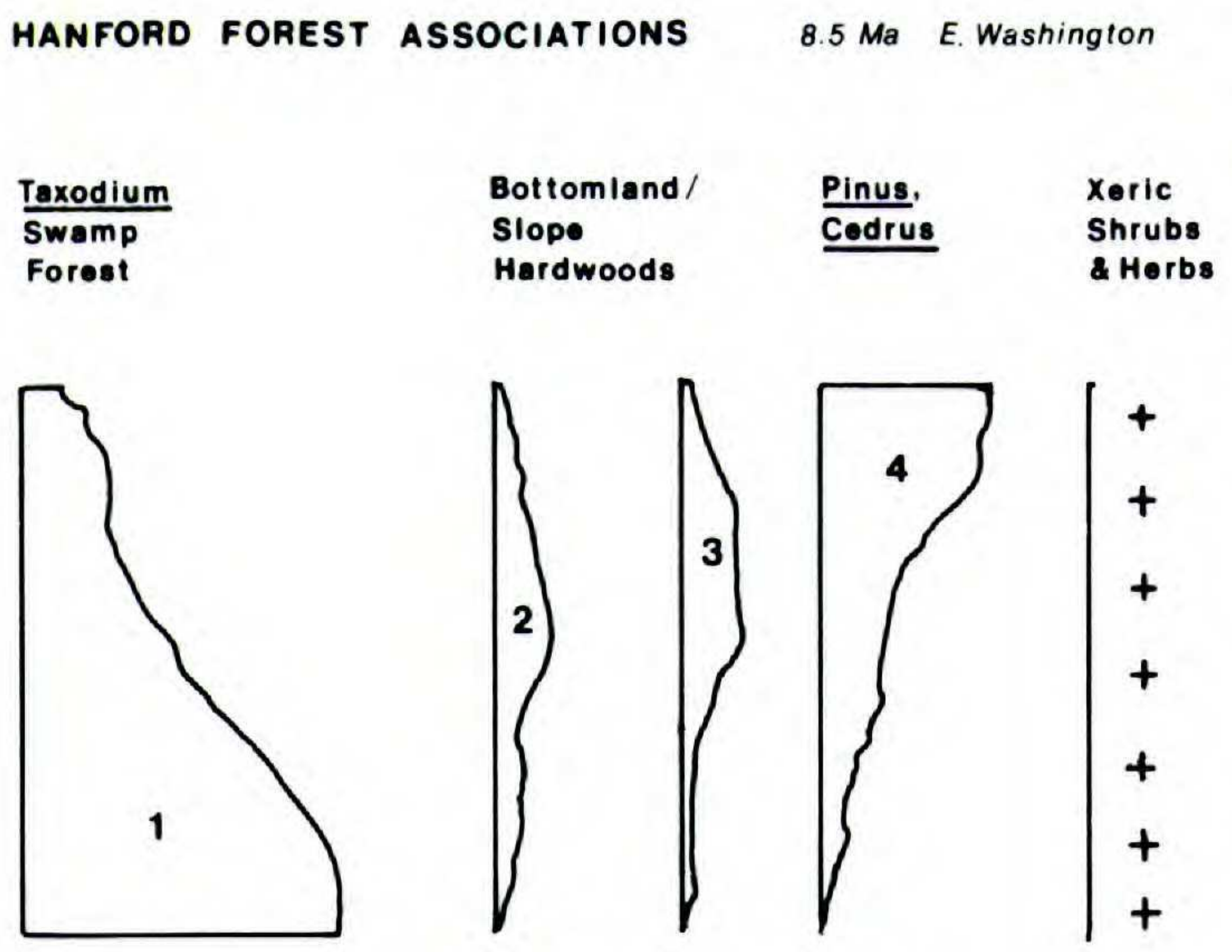


FIGURE 9B. Schematic phases of vegetation shown by Figure 9A pollen diagrams.

Carya, Ulmus-Zelkova, Pterocarya, Sapindaceae, and *Salix.*

(3) *Montane slope forest.* This assemblage is dominated by *Pinus* spp. with important amounts of *Abies, Picea,* and Cupressaceae pollen. *Tsuga, Quercus, Artemisia,* grasses, Onagraceae, and additional herbs may have been locally abundant (Leopold & MacGinitie, 1972: 198).

The proportion of broad-leaved Tertiary relict genera that are now exotic (eastern Asian and eastern American genera such as *Pterocarya, Carya,* and *Ulmus-Zelkova*) obviously is low compared with those in pollen and leaf assemblages of the same time period west of the Rockies (e.g., Hanford, Poison Creek, and Trapper Creek). Except for the "riparian" hardwoods, the flora has a modern aspect indeed, as it compares well with modern pollen rain (see top of Fig. 11).

Four other pollen sites from widely different times in the Miocene are in basins along foothills and in the eastern Rockies of Colorado and Wyoming (Fig. 12; localities in Appendix IV; selected pollen counts in Appendices V, VI; Leopold & MacGinitie, 1972). Early Miocene (Hemingfordian) sites are the Troublesome Formation from Grand County, Colorado (Izett,

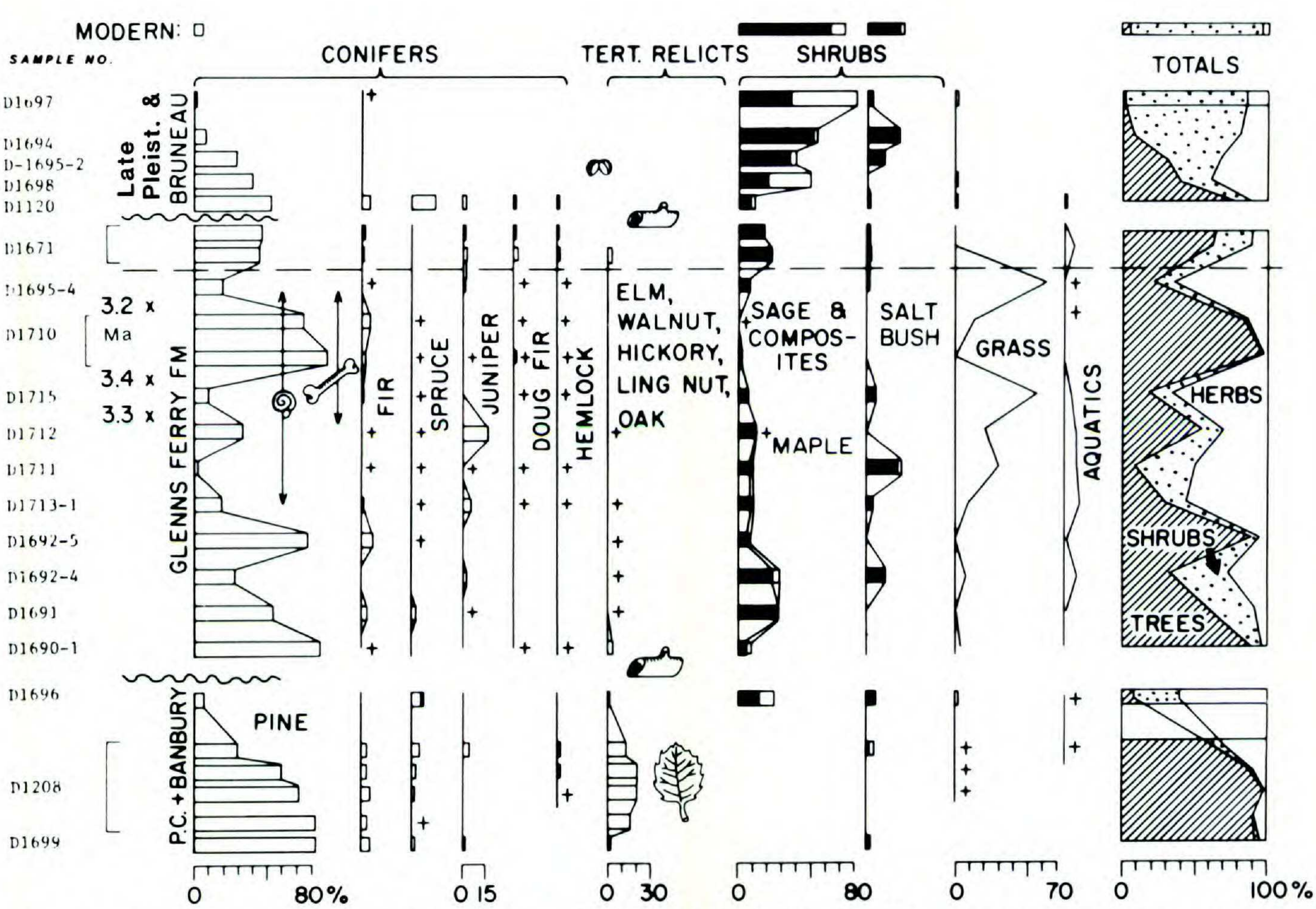


FIGURE 10. Composite pollen diagram, late Miocene to late Pleistocene, Hagerman area, southwestern Idaho. Modern pollen rain at Hagerman is shown at top (from Leopold & Wright, 1985). Fossil wood indicated along the unconformity at the top of the Glenns Ferry Formation is *Quercus,* white oak type (Malde & Powers, 1962). Note that Pleistocene samples D1120 and D1698 are now classified as from Yahoo Clay of late Pleistocene age. Sample D1695-2 is Glenns Ferry Formation (Malde, 1982). Sample D1697 is from a Late Pleistocene buried soil on the King Hill Basalt. Sample D1694 is of the Bruneau Formation of middle Pleistocene age. *Celtis* fruits (see symbol) are of Late Pleistocene age.

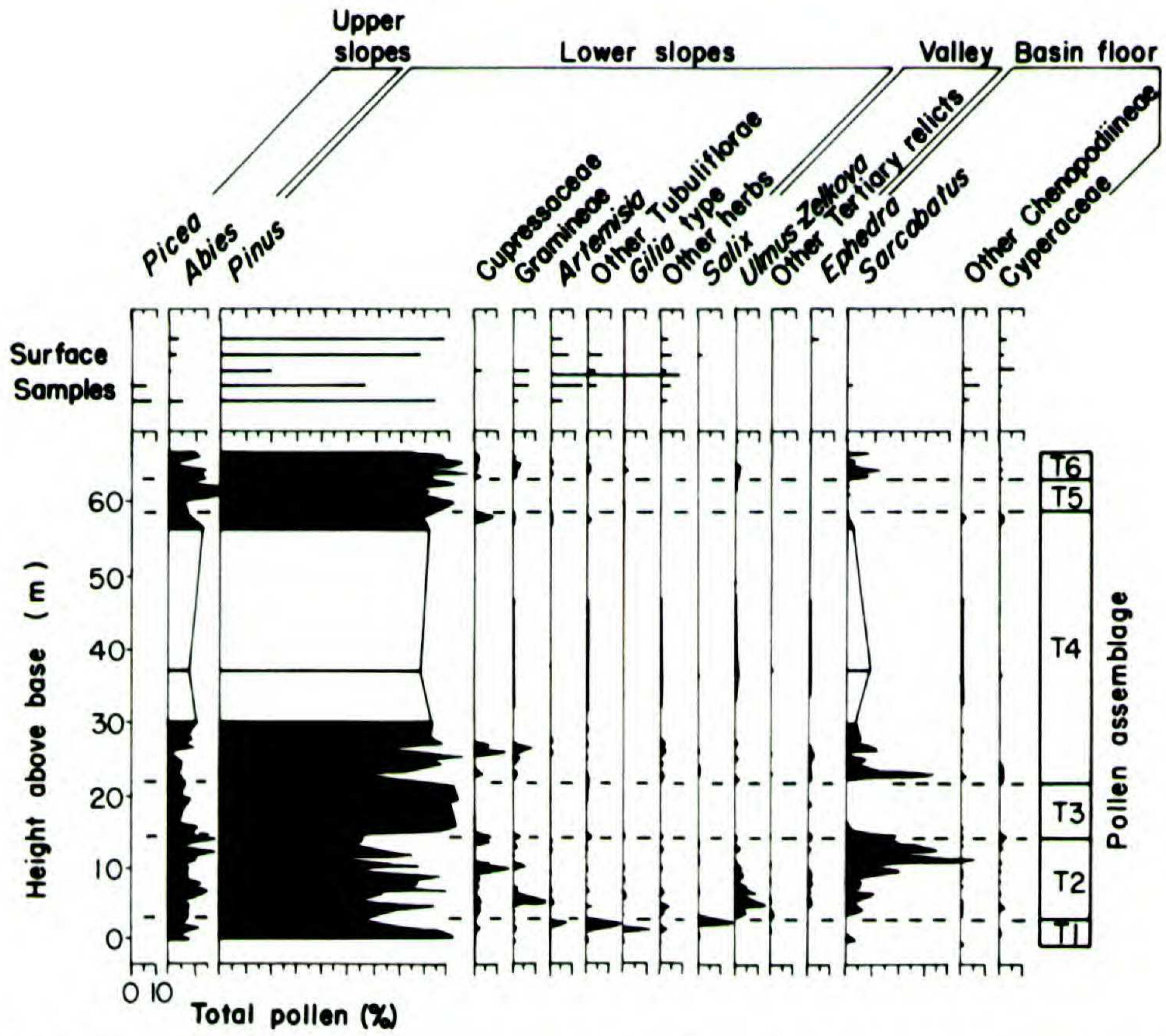


FIGURE 11. Pollen diagram, showing selected types and inferred habitat, upper Teewinot lake beds, Jackson Hole, Wyoming (% total pollen). K/Ar age is 9 Ma or late Miocene (from Barnosky, 1984).

1968), and the Split Rock Formation from the Sweetwater Basin, Natrona County, Wyoming (Love, 1961). A mid-Miocene (Barstovian) site is from the Saratoga Valley, Carbon County, Wyoming. The youngest site, the Moonstone Formation in the Sweetwater Basin, Wyoming, may be of Barstovian or younger age (Robinson, 1971; Love 1961). All are old lake beds near low rolling granite or bedrock hills that probably existed in the Miocene. Pollen is moderately abundant to rare and demonstrates impoverished floras similar to that evident at the Jackson Hole, Wyoming site. Only two types of communities can be conjectured from the data:

(1) *Open basin and lakeside environments* in which *Artemisia, Sarcobatus* and other Chenopodiineae, *Ephedra,* and *Eriogonum* suggest steppic and halophytic environments and in which *Salix,* Betulaceae, and aquatics imply lake-margin or riparian environments. Terrestrial herbs of the Polemoniaceae, Compositae, Onagraceae, Umbelliferae, and Polygonaceae may have grown in these basin environments (Appendix VII).

(2) *Mountain slopes* dominated by *Pinus* with lesser amounts of *Picea, Abies,* and *Juniperus.* Whether *Juglans, Carya, Quercus,* and *Ulmus-Zelkova* were associated with woodland or forest, or whether most of these were restricted to riparian environments cannot be deduced from the available information, though the latter is more probable.

Implications. The consistent presence of xeric and desert-scrub taxa that are sometimes abundant suggests the appearance of steppic vegetation with a diverse herb flora during widely separate times during the Miocene. Grass pollen grains are usually present but never abundant. They are probably associated with depauperate conifer forest or woodland. Several other basin sites in the central and southern Rockies are consistent with the modern aspects of these Miocene floras (Meyer, 1986; Leopold & MacGinitie, 1972).

The Rocky Mountain data stand in stark contrast to the Miocene basin sequences from Idaho westward to eastern Washington where pollen and leaf data alike point to rich forest vegetation containing abundant and diverse deciduous hardwoods. Broad-leaved evergreen trees are apparently absent in the Neogene of the Rocky Mountains.

III. GREAT PLAINS LOCALITIES

Megafossil floras from the Great Plains region (Fig. 7) suggest that prairie elements were present

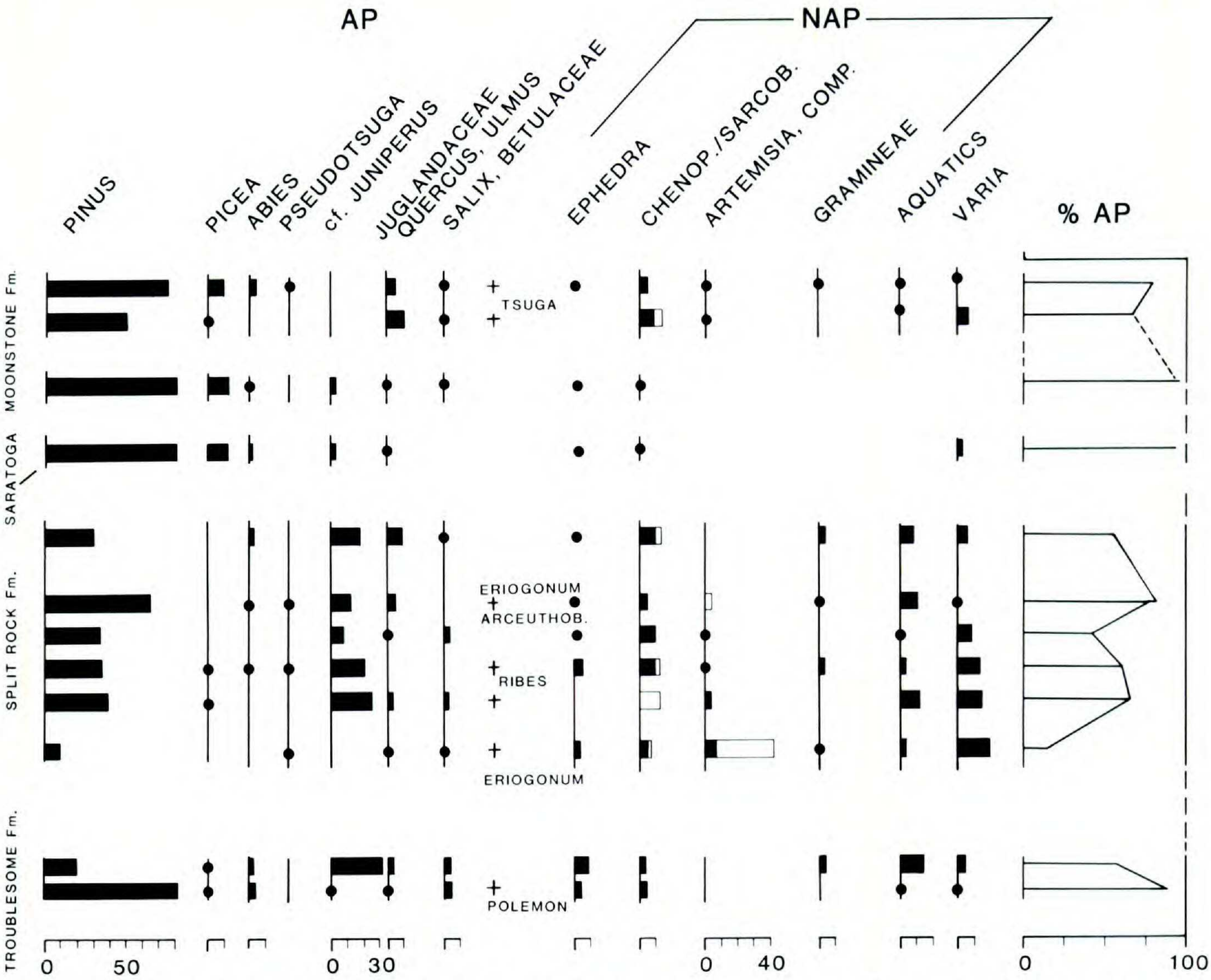


FIGURE 12. Pollen spectra from four Rocky Mountain sites: Troublesome Formation, Colorado, and Split Rock Formation, Wyoming, lower Miocene; Saratoga Valley, Wyoming, mid Miocene; Moonstone Formation, Wyoming, of younger Neogene age (Appendix V, VI).

and that grassland developed to various degrees during the Miocene (Elias, 1942; Chaney & Elias, 1938). An excellent summary by Axelrod (1985) portrays a sequence indicating a generally decreasing precipitation regime from about 16 Ma onward. The older sites are deciduous hardwood forest with prairie elements (Fig. 13). According to Axelrod, the younger sites suggest woodland or riparian border hardwoods with more extensive grassland (Fig. 13).

From the Neogene sediments of the upper Arikaree and Ogalalla groups on the Great Plains and High Plains, Elias (1932, 1935, 1942) made systematic fruit/seed and leaf collections at almost 100 localities from South Dakota to northern Texas. The widespread sediment layers with occasional volcanic ashes and vertebrate fossils provided stratigraphy. Elias undertook to define a sequence of fossil seed zones. Modern dating indicates that the main part of this sequence ranges from Hemingfordian through Hemphil-

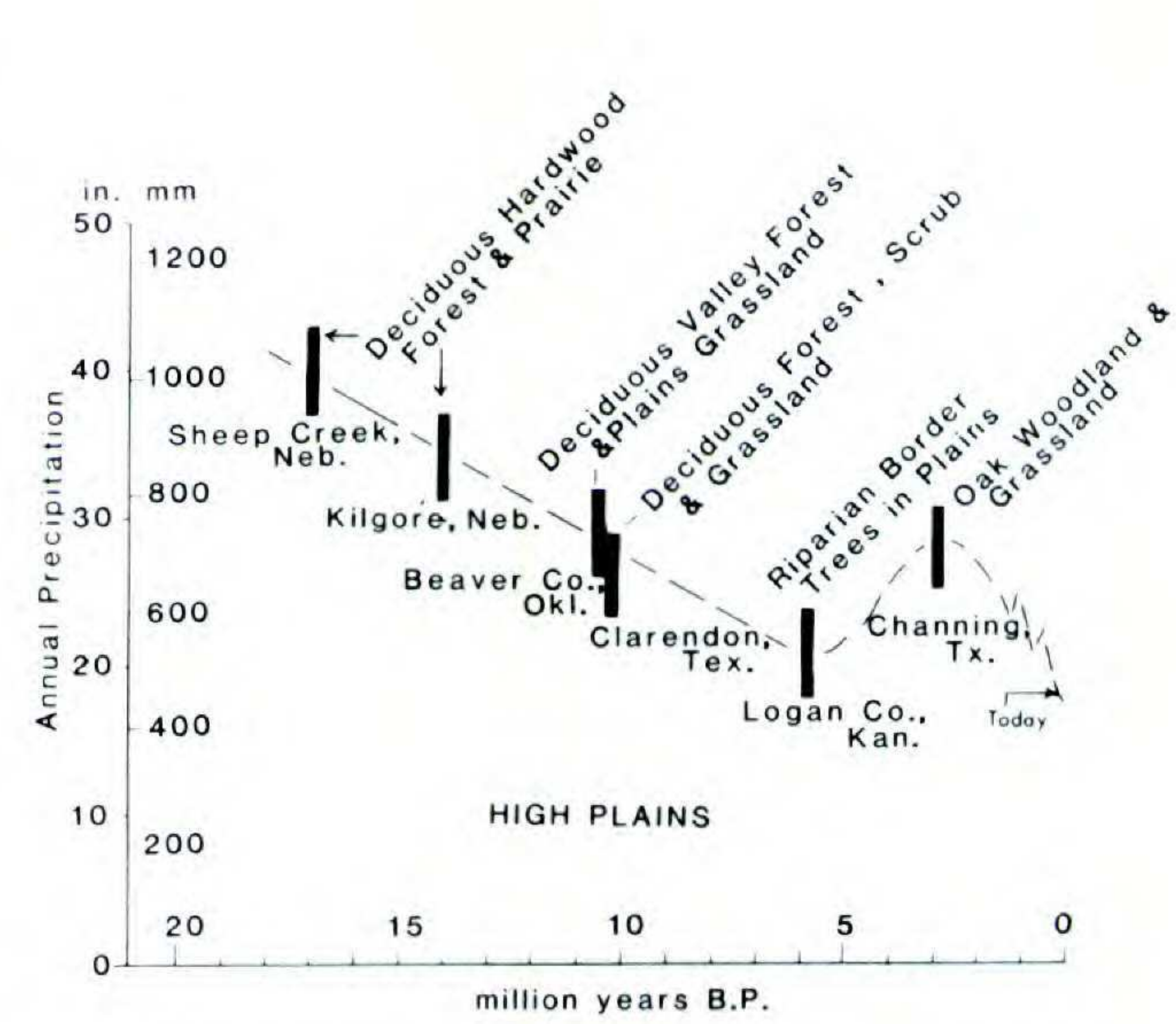


FIGURE 13. Fossil floras from the Great Plains (High Plains of Axelrod, 1979) suggest a gradual reduction in precipitation during the late Tertiary.

TABLE 5. Geographic affinities of the Kilgore flora, Nebraska (15–12 Ma, mid Miocene), showing the representation of its species in Miocene floras of the Columbia Plateaus (after MacGinitie, 1962).

Modern Distribution Groups	Number of Species in Kilgore Flora by Geographic Group	Number of These Species Occurring in Miocene of Columbia Plateaus
East of Rocky Mountains only	10	1
Mexico and southern Rocky Mountains	7	1
Rocky Mountains only	3	0
West of Rocky Mountains	2	0
Split affinities between distinctly eastern and distinctly western species	3	1?
Cosmopolitan	1?	1?
Eastern Asia	2	2
Total number of species:	27–28	4–6 or ca. 18–21%

lian (ca. 18–4 Ma). At most of his sites in the Ogalalla Group (Kilgore and younger age) fruiting parts of grasses and prairie herbs were the most common and in most cases the only fossils, although arboreal leaves were present at a few sites (most of the latter were summarized by Chaney & Elias, 1938, and by Axelrod, 1979, 1985).

Elias's identifications, corroborated in large part by the recent work of Thomasson, demonstrate that ancestral Stipeae appear in the earliest Hemingfordian strata or earlier, and that Boraginaceae (*Biorbia, Krynitzka*) and Paniceae appear consistently and abundantly in Clarendonian (Ash Hollow Formation) sites. Diversity of prairie taxa increases up section.

Perhaps the most surprising feature is the widespread nature of Elias's fossil fruit and seed zones. In Nebraska the following zones range from Kilgore age to Ash Hollow and younger units (Kimball Formation) of the Ogalalla Group (in stratigraphic order; Elias, 1942):

VI. Kimball Formation (calliche).
V. *Biorbia fossilia* with *Krynitzka coroniformis* and *Stipidium grande* (Ash Hollow Formation).
IV. *Krynitzka coroniformis* zone with *Stipidium tubus*.
III. *Stipidium commune* (Valentine Formation).

Elias found the same dominant species at the same zones in the Ogalalla at Wray, Yuma County, and at many other points in eastern Colorado. He found his *Krynitzka* zone underlying the *Biorbia* zone at Wallace County, Kansas (associated with fossil rhinoceros) and at other sites in Kansas. *Biorbia* subzones (not described here) were found in Beaver and Ellis counties, Oklahoma.

The presence of prairie elements during the Miocene has been documented by Thomasson using scanning electron microscopy to identify leaves, anthoecia (lemmas and paleas of grass

TABLE 6. Kilgore species occurring in Miocene floras of the Columbia Plateaus (from MacGinitie, 1962; Edwards, 1983). Question mark indicates probable fossil species, but affinity with modern taxon seems reasonably certain.

Species	Related to
Populus washoensis?	*P. grandidentata* (E U.S.A., SE Canada)
Pterocarya oregoniana	*P. insignis* (E Asia)
Mahonia marginata	*M. bealii* (China)
Cedrela trainii	*C. mexicana* (NW Mexico)
Acer minor?	*A. negundo* (W & E U.S.A. & S Canada)
Fraxinus coulteri?	*F. oregona* (W U.S.A.)
	F. americana (E & central U.S.A., S Canada)
	F. pennsylvanica (E & central U.S.A., S Canada)

spikelets), fruits, and seeds (Thomasson, 1978a, 1978b, 1979, 1980a, 1980b, 1980c, 1983, 1984, 1985; Voorhies & Thomasson, 1979). For assignment of fossil grasses, epidermal patterns and silica bodies (phytoliths) were particularly diagnostic. The plant fossils occurred frequently with vertebrate fossils (rhinoceros, elephantids, horse, and camel). The Ash Hollow Formation (Ogallala Group) in Nebraska, Clarendonian and Hemphillian in age, contains a rich assemblage of prairie plants and aquatics, including representatives of eight plant families (*Chara* sp., Characeae; *Equisetum* sp., Equisetaceae; *Potamogeton* sp., Potamogetonaceae; *Carex gracei* and two other *Carex* spp., *Cyperocarpus pulcherrima,* and *C. terrestris,* Cyperaceae; *Archaeoleersia nebraskensis,* 12 species of *Berriochloa, Nassella* sp., *Oryzopsis* sp., *Paleoeriocoma hitchcockii,* and *Panicum elegans,* Gramineae; *Biorbia, Cryptantha* spp., *Prolappula* sp., Boraginaceae; *Celtis willistonii,* Ulmaceae; and *Polygonum* sp., Polygonaceae). In addition, representatives of the Gramineae (species of *Berriochloa*) and Cyperaceae (*Cyperocarpus eliasii*) have been reported from the Sheep Creek Formation in Nebraska (late Hemingfordian), and new species of the Gramineae (*Berriochloa* spp.) and Boraginaceae (*Biorbia* sp., *Cryptantha* spp., and *Eliasiana* sp.) have been described from the Keller site in Ellis County, Kansas (Hemphillian or Clarendonian).

Although the affinities of most of the fossil species are speculative, those of the grasses appear to be rather straightforward. For example, the fossil grasses are classified in tribes Oryzeae, Stipeae, and Paniceae. *Archaeoleersia* appears to be the forerunner of *Leersia* (tribe Oryzeae) and is most similar to living *Leersia ligularis* and *L. monandra* of North, Central, and South America and to *L. triandra* of Africa (Thomassan, 1980b). *Berriochloa, Nassella, Oryzopsis,* and *Paleoeriocoma* are all classified in Stipeae. *Berriochloa* shows features that suggest it is ancestral in the evolutionary series: *Berriochloa–Piptochaetium–Stipa* (sect. *Hesperostipa*) (Thomasson, 1978a). *Paleoeriocoma,* likewise, belongs to an evolutionary series: *Nassella–Oryzopsis–Stipa*; this genus is found with *Nassella* in deposits and appears to be ancestral to species of *Oryzopsis* (sects. *Eriocoma* and *Oryzopsis*) and possibly to some species of *Stipa* (Thomasson, 1980c). *Panicum elegans* is most similar to extant species of *Dichanthelium* but has not been transferred to that genus due to inadequate sampling of the micromorphological characters of the many species of *Panicum* (Thomasson, 1980b). Tribes Oryzeae and Paniceae, especially, contain grasses of southern affinities; however, the relationships of tribe Stipeae remain uncertain (Barkworth, 1981) even though many extant species have southern affinities. The other families represented in the fossil deposits (Boraginaceae, Cyperaceae, and Ulmaceae) generally are best represented in subtropical or warm regions and, predictably, would have southern affinities.

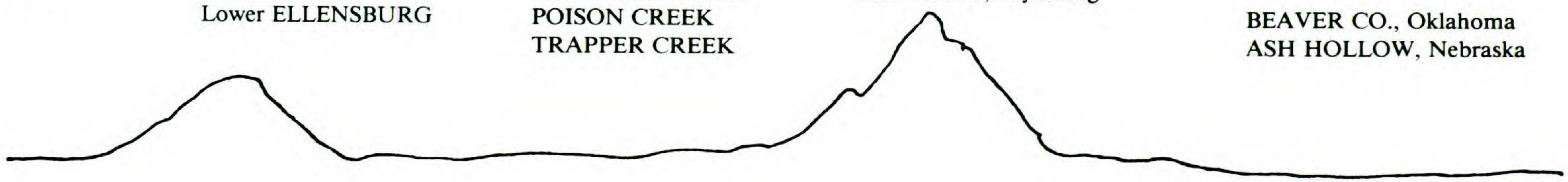
The Kilgore flora of Nebraska is central to our data base since the locality occurs at about the same latitude as the Columbia Plateaus floras. It is of mid-Miocene (Barstovian) age and was well documented by MacGinitie (1962), who provided leaf and pollen data. Hence it can be compared with sites of that age on the Columbia Plateaus. The 28 species MacGinitie identified show the strongest affinity (57%) with modern taxa that grow chiefly east of the Rocky Mountains; secondary affinity is with southerly taxa that now occur in Mexico and the southern Rocky Mountains (20%). Other relationships are minor and include a few species that occur west of the Rocky Mountains: two in eastern Asia, and one cosmopolitan group. Importantly, at least three species are intermediate between distinctly eastern and distinctly western North American taxa: *Fraxinus coulteri, Populus gallowayi,* and *Celtis kansana* (Table 5).

Only six Kilgore species (21%) occur as fossils in the Miocene floras of the Columbia Plateaus (Table 6). These include a mixture of geographic elements, and small east–west differences may occur according to more recent literature. For example, the Kilgore fossil of *Acer is A.* cf. *negundo* var. *negundo,* but the Columbia Plateaus species *Acer negundoides* is morphologically close to *A. negundo* var. *californicum* (J. A. Wolfe, pers. comm., 1986). In summary, the floristic relationship of the Kilgore with the Columbia Plateaus floras is slight.

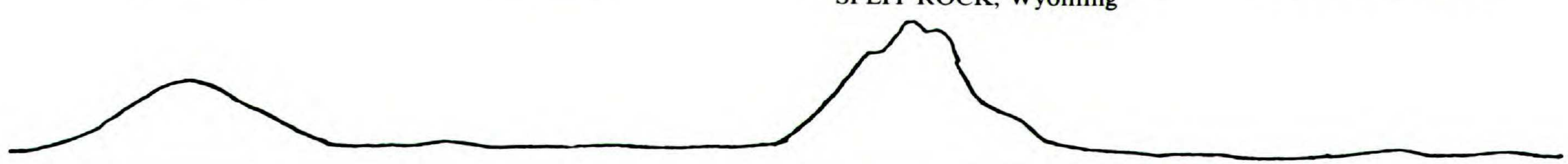
Implications. The mid-Miocene grasses (e.g., Ash Hollow flora) include forms ancestral to those of the present Great Plains grasslands, many with southern affinity. Woody elements (e.g., Kilgore flora) are chiefly related to living taxa of the eastern U.S. The combined data suggest that the Great Plains flora of the mid Miocene was floristically distinct and had little in common with the Columbia Plateaus Miocene floristic province. The Kilgore flora of the Great Plains bears a stronger relationship to Miocene floras of the eastern sea-

TABLE 7. East–west transects of dominant vegetation types across the Rocky Mountain cordillera for two time intervals during the Miocene. Examples of floras are capitalized. Schematic mountain ranges are presumed to be somewhat higher during Clarendonian than before (regional uplift which probably occurred is not drawn here).

	Eastern Washington, Eastern Oregon	Idaho	Rocky Mountain Foothills	Great Plains
Clarendonian	Montane conifer & deciduous forest; *Taxodium* swamp	Montane conifer & deciduous forest	Montane conifer forest with steppe openings	Deciduous valley forest, plains & grassland
8–12 Ma	HANFORD Lower ELLENSBURG	BANBURY BASALT POISON CREEK TRAPPER CREEK	TEEWINOT, Wyoming	BEAVER CO., Oklahoma ASH HOLLOW, Nebraska



Barstovian/Late Hemingfordian	Deciduous hardwood forest & *Taxodium* swamp	Deciduous hardwood forest & *Taxodium* swamp	Montane conifer forest with steppe openings	Deciduous open forest & prairie
12–17 Ma	MASCALL	CLARKIA	TROUBLESOME, Colorado SPLIT ROCK, Wyoming	KILGORE, Nebraska



board, e.g., with Calvert Cliffs, than with floras of the Columbia Plateaus (J. A. Wolfe, pers. comm., 1987).

Kilgore vegetation was in Axelrod's (1985) view probably "a wooded grassland with semi-open grassy forests and woodlands on the interfluves as well as patchy grasslands." The fauna suggests a frost-free climate. This is consistent with MacGinitie's (1962) analysis.

In younger Miocene floras (Clarendonian and Hemphillian, e.g., from Ash Hollow, Nebraska and Beaver County, Oklahoma), seeds of prairie elements are much more abundant and more widespread. Leaf floras suggest that woody vegetation was confined chiefly to valley-bottom and riparian-border habitats. Together these data suggest "either parklands or grasslands" on the interfluves (Axelrod, 1985; 171). Pliocene floras indicate extensive grassland on the Great Plains, although, as Axelrod and MacGinitie pointed out, the evidence is not adequate to establish that pure grasslands occurred before the postglacial.

SYNTHESIS—CONTRASTS EAST AND WEST OF CORDILLERA

From the data presented, dominant vegetation types east and west of the cordillera can be compared for two times during the Miocene. Table 7 summarizes the general picture for the Barstovian/late Hemingfordian (ca. 17–12 Ma) and the Clarendonian (ca. 12–8 Ma). During these two intervals, the Columbia Plateaus west of the Continental Divide consistently maintained deciduous hardwood and montane conifer forests, both rich in woody genera, while evidence from the Great Plains east of the Rockies clearly indicated the existence of deciduous valley forest with grassland elements. Floristically the eastern floras bear little relation to those of the western area. During both of these times the eastern deciduous forest and grassland were separated from forests of the west (1) by the continued existence of the Rocky Mountain massif, which may have become more elevated during the Miocene (Trimble, 1980), and (2) by the continued presence of an impoverished montane conifer forest with steppe elements in the cordilleran area.

Through most of the Miocene there appear to have been floristic provinces distinct from each other:

(1) *The Great Plains province* had its primary affinity with species of the eastern U.S.A. and was floristically distinct from floras of the Columbia Plateaus. It contained elements that later became important forest species of riparian vallies (e.g., American elm) as well as extinct genera ancestral to modern grassland elements (*Berriochloa* and *Archaeoleersia*).

(2) *The Rocky Mountain province* was dominated by depauperate conifer forest or woodland with steppe. Except for infrequent pollen of Juglandaceae, Ulmaceae, and *Tsuga,* the spectra resemble modern pollen rain. The presence of *Tsuga* suggests that the "maritime conifer forest" (of Habeck, 1987) now found near the Canadian border may then have been in a more southerly position. We do not know what species may have been involved, but the impoverished generic list of Pinaceae alone places it in stark contrast with the rich conifer assemblages of the Columbia Plateaus region during the Miocene.

(3) *The Columbia Plateaus province* did not take on a relatively modern character on a generic basis until at least late Pliocene (Blancan) time or possibly even Pleistocene time. Although grassland and steppic elements (e.g., *Artemisia, Sarcobatus*) existed in this region throughout the Miocene, they were unimportant numerically during that period. Judging from the Snake River Plain data, grasses became sporadically abundant in Pliocene (Blancan) time—fully 10 Ma after grassland may have developed in the Great Plains region.

The late appearance of grassland west of the Rocky Mountains may mean that eastern and western grassland provinces are of different origins. Support for this tentative conclusion is derived from the following statement based on data presented earlier in the paper:

(1) Great Plains grassland taxa with southern affinities, now considered ancestral forms, appeared during the Miocene.

(2) The Great Plains floristic province was separated from the Columbia Plateaus during the Miocene by the orographic barrier and by the existence of an impoverished montane conifer forest with steppe on the Rocky Mountain cordillera.

(3) Grasses of northern affinities adapted to summer-dry conditions may have moved into the Columbia Plateaus from the north after the major shift from summer-wet to summer-dry climate about 6 Ma (Hemphillian)—during the demise of the rich Columbia Plateaus hardwood- and certain conifer-forest elements. Floristic evi-

dence confirms the strength of these barriers since Barstovian (mid Miocene) time.

BIOGEOGRAPHIC IMPLICATIONS

The existence of montane conifer forest and steppe on the Rocky Mountain massif throughout the Miocene means that biogeographic connections between the deciduous forests of the Columbia Plateaus and those of eastern U.S.A. were cut off since at least the early Miocene.

Eastern hardwood and swamp elements coexisted on each side of the divide in the Miocene until they were eliminated in the west by the climatic deterioration during Pliocene time.

The important shift to a summer-dry climate came relatively rapidly to the Columbia Plateaus, diminishing a vast reservoir of genetic resources; this included many deciduous and coniferous taxa with affinities to modern taxa of eastern Asia and eastern U.S.A. that show adaptations to a summer-wet climatic regime. This basic change reduced the diversity of the montane coniferous forests of the interior in the Pacific Northwest except along the Pacific coast. It further established conditions in which steppic elements and grassland of northern distribution probably became established and prominent on the Columbia Plateaus.

LITERATURE CITED

ARMSTRONG, R. K., W. P. LEEMAN & H. E. MALDE. 1975. K-Ar dating, Quaternary and Neogene volcanic rocks of the Snake River Plain, Idaho. Amer. J. Sci. 275: 225–251.

AXELROD, D. I. 1964. The Miocene Trapper Creek flora of southern Idaho. Univ. Calif. Publ. Geol. Sci. Ser. V. 51: 1–148.

———. 1979. Desert vegetation, its age and origin. Pp. 1–72 *in* J. R. Goodin & D. K. Northington (editors), Arid Land Plant Resources. Proc. Int. Arid Lands Conf. Pl. Resources. Texas Tech Univ., Lubbock, Texas.

———. 1985. Rise of the grassland biome, central North America. Bot. Rev. 51: 164–201.

BARKWORTH, M. E. 1981. Foliar epidermis and taxonomy of North American Stipeae (Gramineae). Syst. Bot. 6: 136–152.

BARNOSKY, C. W. 1984. Late Miocene vegetational and climatic variations inferred from a pollen record in northwest Wyoming. Science 223: 49–51.

BRYSON, R. A. & F. K. HARE. 1974. Climates of North America. Volume 11 *in* H. E. Landsberg (editor), World Survey of Climatology. Elsevier, Amsterdam.

CHANEY, R. W. 1938. The Deschutes Flora of eastern Oregon. Publ. Carnegie Inst. Wash. 476: 185–216.

——— & D. I. AXELROD. 1959. Miocene floras of the Columbia Plateau, Parts I & II. Publ. Carnegie Inst. Wash. 617: 1–237.

——— & M. K. ELIAS. 1938. Late Tertiary floras from the High Plains. Publ. Carnegie Inst. Wash. 476: 1–46.

CROSS, A. T. & R. E. TAGGART. 1982. Causes of short-term changes in fossil plant assemblages: some considerations based on a Miocene flora of the northwest United States. Ann. Missouri Bot. Gard. 69: 676–734.

DAUBENMIRE, R. 1978. Plant Geography. Academic Press, New York.

DEPARTMENT OF ENERGY. 1986. Environmental Assessment, Reference Repository Location, Hanford Site, Washington, Volume 1. DOE/RW-0070.

EDWARDS, S. W. 1983. Cenozoic History of Alaska and Port Orford *Chamaecyparis* Cedars. Ph.D. Dissertation (Paleontology). Univ. California, Berkeley, California.

ELIAS, M. K. 1932. Grasses and other plants from the Tertiary rocks of Kansas and Colorado. Univ. Kansas Bull. 33: 333–367.

———. 1935. Tertiary grasses and other prairie vegetation from the High Plains of North America. Amer. J. Sci. Ser. 5. 29: 24–33.

———. 1942. Tertiary grasses and other herbs from the High Plains. Geol. Soc. Amer. Spec. Pap. 41.

FIELDS, P. F. 1983. A Review of the Miocene Stratigraphy of Southwestern Idaho, with Emphasis on the Payette Formation and Associated Floras. Ph.D. Dissertation (Paleontology). Univ. California, Berkeley, California.

GRAHAM, A. 1963. Systematic revision of the Sucker Creek and Trout Creek Miocene floras of southeastern Oregon. Amer. J. Bot. 50: 921–936.

———. 1965. The Succor Creek and Trout Creek Miocene floras of southeastern Oregon. Kent State Univ. Bull. Res. Ser. IX, 53: 1–147.

GRAY, J. 1964. Northwest American Tertiary palynology: the emerging picture. Pp. 21–30 *in* L. M. Cranwell (editor), Ancient Pacific Floras. Univ. Hawaii Press, Honolulu, Hawaii.

———. 1985. Interpretation of co-occurring megafossils and pollen: a comparative study. Pp. 185–244 *in* C. J. Smiley (editor), Late Cenozoic History of the Pacific Northwest. A.A.A.S. Pacific Div., San Francisco.

HABECK, J. R. 1987 [1988]. Present-day vegetation in the northern Rocky Mountains. Ann. Missouri Bot. Gard. 74: 804–840.

HITCHCOCK, C. L., A. CRONQUIST, M. OWNBEY & J. W. THOMPSON. 1955. Vascular Plants of the Pacific Northwest, Part 5. Univ. Washington Press, Seattle, Washington.

———, ———, ——— & ———. 1969. Vascular Plants of the Pacific Northwest, Part 1. Univ. Washington Press, Seattle, Washington.

HULTÉN, E. 1968. Flora of Alaska and Neighboring Territories. Stanford Univ. Press, Stanford, California.

IZETT, G. A. 1968. Geology of the Hot Sulphur Springs Quadrangle, Grand County, Colorado. U.S. Geol. Surv. Prof. Pap. 586:1–79.

KNOWLTON, F. H. 1926. Flora of the Latah Formation of Spokane, Washington, and Coeur d'Alene, Idaho. Univ. Wash. Geol. Surv. Prof. Pap. 140A: 17–81.

LEOPOLD, E. B. 1969a. Late Cenozoic Palynology. Pp.

377–438 *in* R. H. Tschudy & R. A. Scott (editors), Aspects of Palynology. John Wiley & Sons, New York.
———. 1969b. Selected pollen and spore types of middle Miocene age from the Troublesome Formation, Granby, Colorado. Pp. 405–407, pl. 17-2 *in* R. H. Tschudy & R. A. Scott (editors), Aspects of Palynology. John Wiley & Sons, New York.
——— & H. D. MacGinitie. 1972. Development and affinities of Tertiary floras in the Rocky Mountains. Pp. 147–200 *in* A. Graham (editor), Floristics and Paleofloristics of Asia and Eastern North America. Elsevier Publ. Co., Amsterdam.
——— & V. C. Wright. 1985. Pollen profiles of the Plio-Pleistocene transition in the Snake River Plain, Idaho. Pp. 323–348 *in* C. J. Smiley (editor), Late Cenozoic History of the Pacific Northwest. A.A.A.S. Pacific Div., San Francisco.
Love, J. D. 1956. New geologic formation names in Jackson Hole, Teton County, northwestern Wyoming. Amer. Assoc. Petrol. Geol. Bull. 40: 1899–1914.
———. 1961. Split Rock Formation (Miocene) and Moonstone Formation (Pliocene) in Central Wyoming. U.S. Geol. Surv. Bull. 1121-I: 1–37.
MacGinitie, H. D. 1933. The Trout Creek flora of southeastern Oregon. Publ. Carnegie Inst. Wash. 416: 23–68.
———. 1962. The Kilgore flora—a late Miocene flora from northern Nebraska. Univ. Calif. Publ. Geol. Sci. 35: 67–158.
McGrew, P. O. 1951. Tertiary stratigraphy and paleontology of south-central Wyoming. Pp. 54–57 *in* Wyoming Geological Association Guidebook, 6th Annual Field Conference, 1951.
McKee, E. H. 1972. Cascadia, the Geologic Evolution of the Pacific Northwest. McGraw-Hill, Inc., New York.
Mack, R. N. & J. N. Thompson. 1982. Evolution in steppe with a few large, hooved mammals. Amer. Naturalist 119: 757–773.
Malde, H. E. 1982. The Yahoo Clay, a lacustrine unit impounded by the McKinney Basalt in the Snake River Canyon near Bliss, Idaho. *In* W. Bonnichsen & R. M. Breckenridge (editors), Cenozoic Geology of Idaho: Idaho Bur. Mines & Geol. Bull. 26: 617–628.
——— & H. A. Powers. 1962. Upper Cenozoic Stratigraphy of western Snake River Plain, Idaho. Bull. Geol. Soc. Amer. 73: 1197–1220.
Meyer, H. W. 1986. An Evaluation of the Method for Estimating Paleoaltitudes using Tertiary Floras from the Rio Grande Rift, New Mexico and Colorado. Ph.D. Dissertation (Paleontology). Univ. California, Berkeley, California.
Neilson, R. P. 1986. High-resolution climatic analysis and southwest biogeography. Science 232: 27–34.
——— & L. H. Wullstein. 1983. Biogeography of two southwest American oaks in relation to atmospheric dynamics. J. Biogeogr. 10: 275.
Robinson, P. 1971. A Geologic Atlas of the Rocky Mountain Region—Tertiary Rocks. Rocky Mountain Assoc. Geol. Publ.
Rogers, K. L., C. A. Repenning, R. M. Forester, E. E. Larson, S. A. Hall, G. R. Smith, E. Anderson & T. J. Brown. 1985. Middle Pleistocene (Late Irvingtonian: Nebraskan) climatic changes in south-central Colorado. Natl. Geogr. Res. 1: 535–564.
Sherman, J. C. 1947. Precipitation of Eastern Washington. Ph.D. Dissertation. Univ. Washington, Seattle, Washington.
Smiley, C. J. 1963. The Ellensburg flora of Washington. Publ. Univ. Calif. Geol. Sci. 35: 159–276.
——— & W. C. Rember. 1985. Composition of the Miocene Clarkia flora. Pp. 95–112 *in* C. J. Smiley (editor), Late Cenozoic History of the Pacific Northwest. A.A.A.S. Pacific Div., San Francisco.
Taggart, R. E. & A. T. Cross. 1980. Vegetation change in the Miocene Succor Creek flora of Oregon and Idaho: a case study in paleosuccession. Pp. 185–210 *in* D. L. Dilcher & T. M. Taylor (editors), Biostratigraphy of Fossil Plants—Successional and Paleoecological Analyses. Dowden, Hutchinson & Ross, Inc., Stroudsburg, Pennsylvania.
———, A. T. Cross & L. Satchell. 1982. Effects of periodic volcanism on Miocene vegetation distribution in eastern Oregon and western Idaho. 3rd Proc. N. Amer. Paleontol. Conv. 3: 535–540.
Tallman, A. M., J. T. Lillie & K. R. Fecht. 1981. Supra-basalt sediments of the Cold Creek Syncline area. *In* W. C. Myers & S. M. Price (editors), RHO-BW-DO-C-60, Rockwell Hanford Operations, Richland, Washington.
Teeri, J. A. & L. G. Stowe. 1976. Climatic patterns and the distribution of C_4 grasses in North America. Oecologia 23: 1–12.
Thomasson, J. R. 1978a. Epidermal patterns of the lemmas in some fossil and living grasses and their phylogenetic significance. Science 199: 975–977.
———. 1978b. Observations on the characteristics of the lemma and palea of the late Cenozoic grass *Panicum elegans*. Amer. J. Bot. 65: 34–39.
———. 1979. Angiosperms from the late Tertiary Keller local fauna of Ellis County, Kansas. Contr. Geol. Univ. Wyoming 17: 59–63.
———. 1980a. A fossil *Equisetum* sp. (family Equisetaceae, subgenus *Hippochaetae*) from the late Tertiary Ash Hollow Formation of Nebraska. Amer. J. Bot. 67: 125–127.
———. 1980b. *Archaeoleersia nebraskensis* gen. et sp. nov. (Gramineae–Oryzeae), a new fossil grass from the late Tertiary of Nebraska. Amer. J. Bot. 67: 876–882.
———. 1980c. *Paleoeriocoma* (Gramineae, Stipeae) from the Miocene of Nebraska: taxonomic and phylogenetic significance. Syst. Bot. 5: 233–240.
———. 1982. Fossil grass anthoecia and other plant fossils from arthropod burrows in the Miocene of western Nebraska. J. Paleontol. 56: 1011–1017.
———. 1983. *Carex graceii* sp. n., *Cyperocarpus eliasii* sp. n., *Cyperocarpus terrestris* sp. n., and *Cyperocarpus pulcherrima* sp. n. (Cyperaceae) from the Miocene of Nebraska. Amer. J. Bot. 70: 435–449.
———. 1984. Miocene grass (Gramineae: Arundinoideae) leaves showing external micromorphological and internal anatomical features. Bot. Gaz. (Crawfordsville) 145: 204–209.
———. 1985. Tertiary fossil plants found in Nebraska. Natl. Geogr. Soc. Res. Rep. 19: 553–564.
Trimble, D. E. 1980. Cenozoic tectonic history of the Great Plains contrasted with that of the south-

ern Rocky Mountains: a synthesis. Mountain Geologist 17: 59–68.

U.S. GEOLOGICAL SURVEY. 1981. Atlas of the United States. Reston, Virginia.

VOORHIES, M. R. & J. R. THOMASSON. 1979. Fossil grass anthoecia within Miocene rhinoceros skeletons: diet in an extinct species. Science 206: 331–333.

VOSS, E. G. 1972. Michigan Flora, Part 1. Cranbrook Inst. Sci., Bloomfield Hills, Michigan.

WOLFE, J. A. 1969. Neogene floristic and vegetational history of the Pacific Northwest. Madroño 20: 83–110.

———. 1978. A paleobotanical interpretation of Tertiary climates in the northern hemisphere. Amer. Sci. 66: 694–703.

APPENDIX I. Pollen records showing occurrence of shrubs, terrestrial herbs?, and herbaceous aquatics in Late Cenozoic samples from Idaho, eastern Oregon, and eastern Washington. Numbers show maximum values in pollen/spore counts; + indicates presence.

	MIOCENE														
	Middle									Late			PLIOCENE	QUATERNARY	
	Mascall[1]	Blue Mountain[1]	Succor Creek[2]	Clarkia[3]	Stinking Water[1]	Miocene, Oregon[4]	Pliocene, Oregon[4]	Trapper Creek[5]	Poison Creek[6]	Jenny Creek[6]	Hanford[6]	Banbury Basalt[6]	Glenns Ferry[7]	Bruneau[6]	Late Pleistocene, Idaho[6]
SHRUBS															
Ephedra	+		+		+	+			+		1				
cf. *nevadensis*				+						+			2	4	+
cf. *torreyana*										+		+	+		
Alnus	+	+	+	5	+					+	4	+	1		1
Chenopodiineae		+	+	1	+?						+	7	20	20	3
Sarcobatus			+		+?			+	2	4	3	1	7		1
Compositae															
Artemisia			+							+	+	14	30	52	36
Elaeagnus											+	+			
Shepherdia			+	+		+									
Rosaceae											+		3		
Cercocarpus										+					
Ilex	+	+	+	+							+				
Rhus				+											
Corylus		+		1	+						+				
Myrica				+							+				
Malvaceae			+								+		+		
Myrtaceae													+		
Yucca type													+		
Ericales											+				
Vaccinium	?	?	+								+				
Caprifoliaceae			+												
Viburnum											+				
Symphoricarpos											+				
Sapindaceae											+				
Mahonia			+												
Cornus			+												
TERRESTRIAL HERBS?															
Compositae undet.			+		+							9	11	2	49
Liguliflorae							+				+		1		
Tubuliflorae											3		6		
Ambrosia			+								+		4		+

APPENDIX I. Continued.

	MIOCENE														
	Middle									Late					
	Mascall[1]	Blue Mountain[1]	Succor Creek[2]	Clarkia[3]	Stinking Water[1]	Miocene, Oregon[4]	Pliocene, Oregon[4]	Trapper Creek[5]	Poison Creek[6]	Jenny Creek[6]	Hanford[6]	Banbury Basalt[6]	PLIOCENE Glenns Ferry[7]	QUATERNARY Bruneau[6]	Late Pleistocene, Idaho[6]
Cruciferae												+	+	11	7
Acalypha type				+											
Onagraceae			+		+					+	+	+			
Polemoniaceae									1		+		4		1
Gilia type											+				
Navarretia											+				
Caryophyllaceae		+			+?										
Stellaria											+				
Gramineae	+	+	+	+	+					+	+	1	75		2
Polygonum cf. *californicum*							+				+				
Eriogonum										+	+		1		1
Anemone													+		
Aizoaceae type													+		
Pachysandra	+		+												
Umbelliferae	?		+												
Ferns	+	+		+	+				+		10	1	1		1
AQUATIC HERBS															
Typha	+	+	+	+	+								+		
Cyperaceae				+						+	10		4		
Scirpus													+		1
Potamogeton			+		+					1		+	1		1
Sparganium		+?			+?								+		
Lemna													5		
Nuphar													+		
Nymphaea													1		
Myriophyllum		+											+		

[1] Jane Gray in Chaney & Axelrod, 1959.
[2] Taggart & Cross, 1980; Graham, 1963.
[3] Gray, 1985.
[4] Gray, 1964.
[5] Leopold & MacGinitie, 1972.
[6] This paper.
[7] Leopold & Wright, 1985.

APPENDIX II. Selected pollen counts, Snake River Plain, Idaho (Fig. 10). Localities given in Leopold & Wright, 1985; the Jenny Creek Formation locality was previously considered as "Salt Lake Formation."

USGS Paleobot. Loc.:	Poison Creek Formation* D1699	Jenny Creek Formation D1208-3	Banbury Basalt D1696
Pinus	84.5	30.2	7.2
Picea	1.0	6.0	
Abies cf. *grandis*	5.4	3.6	
A. cf. *lasiocarpa*	1.0	+	
Pseudotsuga		1.2	
Juniperus	1.0	4.2	
Populus		1.8	
Betula		1.8	0.8
Quercus		4.8	
Alnus			+
Subtotal:	92.9	53.6	8.0
Cedrus-type	0.5		
Carya	0.5	1.8	
Juglans		1.8	+
Pterocarya		0.6	
Ulmus-Zelkova		10.1	0.8
Subtotal Tertiary relicts:	1.0	14.3	0.8
Acer			0.4
Ephedra cf. *torreyana*		0.6	0.8
Ephedra (White R. type)	0.5		
Sarcobatus	2.0	4.2	0.8
Other Chenopodiineae			6.8
Artemisia			14.0
Other Compositae			9.3
Cercocarpus type		0.6	
Elaeagnus			+
Subtotal shrubs:	2.5	5.4	32.1
Polemoniaceae	0.5		
Gramineae		0.6	1.3
Monocots	1.0	4.8	
Cruciferae			0.4
Dicots	2.0	11.9	0.8
Potamogeton		0.6	+
C3P3			56.4
Lycopodium			+
Onagraceae			+
cf. *Parthenocissus*			+
Fern spores	1.0	8.9	1.0
Subtotal NAP:	4.5	26.8	59.9
Total percent	100.9	100.1	100.8
Total tally	(202)	(336)	(236)
Cysts	0.5	1.2	
Botryococcus	12.0		

* Fossil leaves from the Poison Creek Formation identified by J. A. Wolfe (pers. comm., 1987) include *Quercus prelobata* Condit. and *Q.* cf. *chrysolepis* Liebm.

APPENDIX III. Revised list of the Deschutes flora, northern Oregon (after Chaney, 1938, with additions from J. A. Wolfe, pers. comm., 1987; Wolfe includes certain collections made by R. W. Brown from Chaney's floral horizon but a few miles away).

Acer negundoides
Quercus prelobata
Populus washoensis
Populus alexanderi (*P.* aff. *trichocarpa*)
Prunus irvingii (*P.* aff. *emarginata*)
Salix sp. (*S.* cf. *florissantii* of Chaney)
Salix aff. *caudata*
Ulmus affinis Tanai & Wolfe

APPENDIX IV. Localities of selected pollen samples from Wyoming and Colorado (Figs. 6, 12).

Formation	USGS Paleobotany Locality	Site Description
Split Rock	D1309	Type section: SE ¼ NE ¼ Sec. 25, T. 29 N, R. 89 W, Natrona Co., Wyoming. Limestone at top of pumicite, from unit 21 of J. D. Love (1961). Vertebrates from the Split Rock type area are of Hemingfordian age.
Split Rock	D3319	Upper part of formation, 2,650 ft. EWL 600 ft. SNL Sec. 36, T. 27 N, R. 85 W, Carbon Co., Wyoming. J. D. Love measured section L63-11. Sample B & C are 6 and 12 ft. above base of his unit 3. Sample D/E from his unit 4. Samples higher in this unit contain abundant reworked Cretaceous pollen.
Saratoga unit	D1540	Saratoga Valley, radioactive oil shale. SW ¼ NW ¼ Sec. 26, T. 18 N, R. 84 W, Carbon Co., Wyoming. J. D. Love locality L59-49. Associated with vertebrates of Barstovian age according to McGrew (1951).
Moonstone	D1308	Type section; white tuff and white laminated shale. Sec. 17, T. 30 N, R. 89 W, Natrona Co., Wyoming. Samples 1 and 2 are from Love's (1961) unit 16 and 17, respectively.
Troublesome	D3473	Rock Creek facies. NW ¼ SW ¼ Sec. 32, T. 2 N, R. 79 W, Kremmling quadrangle, Grand Co., Colorado. Glen Izett loc. G-63-303 and -304. Sample A is 18 ft. above sample B. Vertebrates from the lower and upper parts of the formation correlate respectively with the lower and upper Hemingfordian Group of Nebraska (Izett, 1968).
Troublesome	D1905	SW ¼ NE ¼ Sec. 29, T. 2 N, R. 79 W, Kremmling quadrangle, Grand Co., Colorado. Carbonaceous bed interbedded with silt lake facies containing mid Miocene vertebrates. Izett coll. G-0153-62.
Troublesome	D3493	NE ¼ SE ¼ Sec. 28, T. 3 N, R. 80 W, Gunsight Pass, Twin Peaks, Kremmling quadrangle, Grand Co., Colorado. Izett loc. G-63-305.

APPENDIX V. Pollen counts, Troublesome Formation, Grand County, Colorado (Figs. 6, 12). Percent pollen and spores. Small counts (shown in parentheses) indicate comparative abundance; + records taxa seen but not in tally.

USGS Paleobotany Locality:	D3473		D3493	D1905
	-b	-a		
Pinus	18.0	72.0	(105)	(62)
Abies sp.	1.3	1.3	(1)	
A. cf. *lasiocarpa*		0.7		
A. cf. *grandis*	+			(1)
Picea sp.	0.7	1.3	(6)	(12)
P. cf. *engelmannii*				(27)
Juniperus type	32.4	0.7		
Ephedra cf. *nevadensis*	8.0	2.7		(1)
Ephedra cf. *torreyana*	+	0.7	(1)	
Ephedra (short axis type)	+			
**Juglans*	+	0.7		
**Pterocarya*	1.3			
**Carya*	+	0.3		
**Ulmus-Zelkova* 4–5 pored	0.7	1.1		(1)
6 pored	+			
Acer	+			
cf. *Populus*	+			
Betula		0.7		
Subtotal trees:	62.4	82.2		
Elaeagnus	+	0.7		
Alnus	1.3	3.2		
Salix	1.3			
Sphaeralcea	0.3	0.7		
Caprifoliaceae				
Lonicera	0.3			
Symphoricarpos	0.3	0.7		
Chenopodiaceae	4.6	2.7	(3)	(1)
Sarcobatus				
cf. *vermiculatus*	0.7			(3)
Compositae	+		(1)	
Artemisia	+	0.7	(3)	
Xanthium type				(1)
Gramineae	1.3	1.1		(1)
Umbelliferae	0.7			
Polemoniaceae		0.3		
Dipsacaceae?	+			
Labiatae	0.3			
Arceuthobium		0.3		
Apocynaceae	+			
Claytonia type	+	0.7		
Sparganium		1.1		
Dicots	3.4	2.0		
Monocots	16.6		(4)	
Botrychium type			(4)	
Riccia type	+			
Trilete spores	7.4	2.7	(2)	
Total percent	100.9	99.1		
Total tally	(300)	(300)	(130)	(110)

* Genera now exotic to Colorado.

APPENDIX VI. Selected pollen counts, Natrona and Carbon counties, Wyoming (Figs. 6, 12). Percent pollen and spores: + records taxa seen but not in tally.

Stratigraphic Unit:	Split Rock				Saratoga	Moonstone	
USGS Paleobotany Locality:	D1309	D3319			D1540	D1308	
		-B	-C	-D/E		-1	-2
Pinus	8.3	39.5	35.3	51.5	80.0	53.0	72.0
Abies spp.				0.8			
cf. *concolor*							2.6
cf. *lasiocarpa*							2.0
cf. *grandis*			0.6		1.3		
Picea spp.		0.5	1.2			1.1	
cf. *engelmannii*					3.6		5.2
cf. *pungens*					7.6		4.6
**Tsuga*							
cf. *mertensiana*							0.4
cf. *heterophylla*							0.4
Pseudotsuga							
cf. *menziesii*	0.8			1.2		1.1	0.4
Juniperus type	0.4	20.5	20.7	7.4	1.8		
Quercus	1.2	1.0		0.4	0.4?		
Populus	+	0.5	0.6				
**Carya*		1.0					0.4?
**Juglans*		0.5					0.4
*cf. *Liquidambar*							1.2
**Ulmus-Zelkova*	0.4	1.0		1.6	0.9	12.5	3.1
Betula	0.4					3.2	
Salix		0.5		0.4			
**Ostrya-Carpinus*						0.5	3.2
Subtotal trees:	11.5	65.0	58.4	63.3	95.6	71.4	95.9
Alnus	0.4			0.4		1.1	0.8
Chenopodiineae	5.0	1.0	9.5	4.7		8.5	1.8
Chenopodium type	0.4						
Sarcobatus	2.1	6.0	1.8		0.9	7.4	1.2
Ephedra							
cf. *torreyana*		+	1.2	0.8	0.4		0.4
cf. *nevadensis*	0.4	1.5	4.1				
Compositae	7.5	0.5		1.2			
Liguliflorae		0.5	0.6				
Artemisia	42.4			1.2		1.1	
Ambrosia	0.8	0.5					
Sapindaceae		0.5					
Ribes		1.0					
cf. *Ptelea*	0.4						
Arceuthobium				0.4			
Caprifoliaceae type			0.6				
Eriogonum	0.4			0.4			
Gramineae	0.4	1.5	1.8	0.4			0.4
Umbelliferae		0.5					
Cruciferae				0.4			
Sparganium		1.5	0.6	0.8			
Cyperaceae	+	0.5	1.8	0.8			
Scirpus			2.4				
CP_3	4.5						
C_3	15.4	2.5		5.1			
Monocots		9.0	13.0	6.6		1.1	

APPENDIX VI. Continued.

Stratigraphic Unit:	Split Rock				Saratoga	Moonstone	
USGS Paleobotany Locality:	D1309	D3319			D1540	D1308	
		-B	-C	-D/E		-1	-2
Dicots	3.3	4.0		0.4		5.3	
Indeterminate	2.9	4.5	0.6	5.7	3.1	3.2	2.4
Fern spores	1.8	3.0	2.4	7.8		1.1	
Total percent	99.6	103.0	98.8	100.4	100.0	100.2	102.9
Total tally	(245)	(208)	(169)	(257)	(223)	(188)	(251)
Reworked pollen		21	3	28			
Botryococcus			++				

* Genera now exotic to Wyoming.

APPENDIX VII. Pollen records showing occurrence of shrubs, terrestrial herbs?, and herbaceous aquatics in pollen samples from the Mio-Pliocene of the central Rocky Mountains. Maximum values, % pollen and spores. + indicates presence or less than 1%.

	Troublesome	Split Rock	Teewinot	Saratoga	Moonstone
SHRUBS					
Ephedra					
cf. *nevadensis*	8	4	3		
cf. *torreyana*	1	1	1	1	1
Alnus	3	+	2		1
Sphaeralcea	1				
Chenopodiaceae	5	10	3		9
Sarcobatus	1	6	70	1	7
Compositae					
Artemisia	1	42	55		1
Elaeagnus	1				+
Caprifoliaceae		1			
Lonicera	+				
Symphoricarpos	1				
Ribes		1			
Ptelea type		+			
Yucca type			3		
TERRESTRIAL HERBS?					
Compositae					
Liguliflorae		1	4		
Tubuliflorae	1	8	15		
Ambrosia		1			+
Xanthium type	1				
Polemoniaceae	1				
Gilia type			11		
Cruciferae		+			
Claytonia type	1				
Onagraceae			+		
Polygonaceae			+		
Eriogonum		1			+
Umbelliferae	1	1			
Apocynaceae	+				
Labiatae	+				
Dipsacaceae	+				
Gramineae	1	2	15		+
Ferns	7	3			1
HERBACEOUS AQUATICS					
Cyperaceae		2	+		
Sparganium	1	2			
Scirpus		2	+		